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Thesis

THE FACTORS INVOLVED IN POLLINATION

Submitted by

Edna Mary Fielding

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OUTLINE

INTRODUCTION

For untold centuries men have sowed their seeds and gathered their crops, never wondering how their seeds were formed nor why they germinated. However, discoveries pointing to the existence of sex in plants were evidently made very early in human history. The existence of fertile and sterile trees of the date palm, was known to the peoples of Egypt and Mesopotamia from the earliest times, and records of the cultivation of these trees and of artificial pollination, found in the palace of Sargon at Khorsabad, have come down to us on bas reliefs from before 700 B.C.

In this embryonic stage the knowledge of pollination was destined to rest for twenty centuries, for it was not until 1632 that the matter was further investigated. In that year Nehemiah Grew published a treatise in which he makes the following statement: " in order that a seed may form, the pollen of a flower must reach its ovule. Without such contact the ovule would never develop into a seed, but would wither and come to nought."* But this guess, though it proved correct in the main, was not supported by any experimental evidence.

About twenty years later Rudolph Camerarius of Tübingen investigated the problem and experimented with the plants themselves. The results of these experiments he summarized in the following words: " in the vegetable kingdom there is accomplished no re-

*Gibson -- Blossom Hosts and Insect Guests- page 3

production by seeds, that most perfect gift of nature, and the usual means of perpetuating the species, unless the previously appearing apices of the flower have already prepared the plant; therefore, it appears reasonable to attribute to these anthers a noble name and the office of male sexual organs. "* But little notice was taken of his work, and practically no progress was made in this new branch of biology till 1732, when the great Swedish naturalist, Linneus, again called attention to this theory and published numerous proofs of his own. The inferences of these three biologists regarding the process of pollination of the stigma is perfectly clear from their statements. The stamens in most flowers were observed to surround the pistil, "and, of course, the presumption was that they naturally shed the pollen upon the pistil."* So the functions of the stamens and pistil were determined; but what relation did color, fragrance, honey, and insect association bear to the problem of seed production?

The part played by insects was first considered in 1761, when J.G. Koelreuter of Karlsruhe, published an account stating that the pollen necessary for fertilization is often brought to the stigma by insects. Thus he opened up a field of research which was cultivated with such splendid result by Konrad Sprengel, thirty years later. Sprengel observed that the bees and other insects seemed to prefer those flowers which posses color, honey, and perfume, and neglect the others. In 1787 he brought out a volume proving that the insects transport the pollen from stamens

*Science -- February 27, 1914--page 299
*Faulkner -- Mysteries of the Flowers--page 17

to pistil, but in the case of most plants with inconspicuous flowers this service is performed by the wind.

Sprengel's theory was a new and startling one, based upon the numerous observations and experiments, " a very beautiful speculation which explained the purpose of the hitherto mysterious lure of the flowers."* Although he had discovered the use of the colors, odors, and forms of the flowers, he failed to discover why cross-pollination was beneficial: and this omission was for several generations fatal to his work. But he had only half solved the problem and only half discerned the truth, for instances were pointed out in which flowers concealed their pollen, or bore stamens and no pistils, and <u>vice versa</u>. His theory was discredited and the riddle of pollination remained unanswered for nearly a hundred years.

Grew and Sprengel had partly solved the mystery and in 1859 Darwin lifted the veil completely. In his experimenting he found that frequent crosses increased both the vigor and productiveness of the plant; and that an occasional cross was almost indispensable. He stated that the principal agents which nature uses for this purpose are insects, birds, wind, and water. The importance of cross-pollination was so impressed on his mind that he closed his famous book on orchids by these words:"Nature abhors perpetual self-fertilization."* "The charm," says Mueller, "was now broken, and the value of Sprengel's work was at once recognized." "The merits of poor old Sprengel, "says Darwin in his autobiography, "so long overlooked, are now fully recog-

* Faulkner -- Mysterious Lure of the Flowers -- page 3
* Darwin -- Cross Fertilization in the Vegetable Kingdom --Page 458

nized many years after his death." By his experimenting Darwin showed beyond doubt that "not only did the bees and insects carry the pollen of flowers, but they carried it from the anthers of one flower to the pistil of another: that this plan gave vigor and adaptability to the species, and that many flowers possessed ingenious mechanisms to protect their stigmas from the touch of their own pollen and to insure the transportation of it to another plant."* This process Darwin called "cross-fertilization." So was the secret of pollination at last revealed.

Many investigators were stimulated by Darwin's book, among these were: Delpino in Italy (1868-1869), Axell in Sweden (1868) Hildebrand in Germany, Asa Gray in North America, and Hans Mueller, brother of Fritz, became a noted authority on cross-fertilization, for his first book, "The Fertilization of Flowers" won the praise of Charles Darwin and is now used as a source for material on pollination. Since Mueller's death in 1883 the best work on pollination has been that of Paul Knuths. He wrote an encyclopedia in five volumes called "The Handbook of Flower Pollination." This is an excellent work describing the floral mechanisms of many plants with a list of their insect visitors.

*Darwin, Charles -- Cross Fertilization in the Vegetable Kingdom -- Page 450

FLOWERS AS REPRODUCTIVE STRUCTURES

Description of a Typical Flower -

Flowers are whorls of modified leaves which are involved in producing seeds, the seed manufactories of plants. This is the purpose of the flowers, and not, as commonly believed, contrived for the pleasures of human beings, to give beauty to the landscape, or to furnish food for insects.

Faulkner describes the world of flowers as a busy modern town. The simile is apt; for as he himself pictures the scene, "The flowers are the shop-keepers who deal in nectar and in pollen, and these they advertise in gaudy, flaming placards about their entrances--blotches and streaks of vivid colors--honey guides, we call them--which are veritable posters to attract the eye from afar. Then to greet the coming purchaser, they put forth easy landing-stages, for their guests are living aeroplanes who must furl their wings before entering. Then, too, the merchandise must be kept away from dew and rain, so the flowers set up ingenious rain shelters of varied form. Lastly, there must be protection against unwelcome guests, veritable shoplifters, and for these the flowers provide bristly traps and such devices."*

"A living machine for making seeds,"* the flower has been called. It is a structure formed for the purpose of pollination, which is the first step in the process of production of seed.

*Faulkner -- Mysteries of the Flowers -- page 28
*Current Literature -- December 1902 -- page 730

It consists of a shortened stem with spore-bearing organs, which, in the majority of cases, are subtended by one or more leaf-like structures. In the typical flower, there are four whorls, the outer whorl of flower-leaves is the calyx, generally greenish, each individual leaf being a sepal. Within this is the corolla, made up of separate leaves in most cases, which are called petals, often bright colored and showy. The calyx and corolla together comprise the perianth. Within the c orolla are the stamens, the male whorl, each of the stamens is composed of a slender stalk, the filament, and a spore-bearing body which are the anthers. The spores are known as microspores. The pistil, the female whorl, is found in the center of the flower; a simple pistil or one of a compound pistil is a carpel. A pistil usually consists of an enlarged base, the ovary, and a slender upper part, the style, which is surmounted by the larger and sticky stigma. The ovary, the principle part of the pistil, is made up of ovules, within each of which is the embryo sac. This embryo sac develops into a female gametophyte. After fertilization, the two gametes, male and female, unite which results in the embryo seed. At the base of the axis is an enlargement known as the receptacle.

These whorls are often very difficult to detect. Through evolutionary processes, the petals in many species have been partly or wholly fused, as in the bellflowers.

The petals of the flowers in the orchids and pea family have lost their symmetry and regularity and are greatly twisted and distorted. Some flowers, such as shown in the daisy family, are crowded together in the smallest possible space and are surrounded by a green dentilled wall of small leaves or bracts. These green bracts are replaced by brilliant red and purple leaves in the poinsettia.

The majority of flowers are monecious, that is, having the stamens and pistils in the same flower; others are, however, dioecious, having stamens and pistils in separate flowers. To fertilize the ovules of the pistil with the pollen grains of the stamen and thus to initiate the "promise of the plant that is to be," is one of the most fascinating studies of the plant world. We accordingly turn to a consideration of methods and instruments used in solving the problem of pollination.

Origin of Floral Structures -

The organs of the flower which are directly or indirectly concerned with pollination form the most complicated part of the flower and hence their origin is difficult to explain. Not only are the flowers complex but also the mouth parts of visiting insects, which are obviously related to this complexity. It is also very difficult to explain the reciprocal symbiosis between flowers and insect, e.g., in the fig and yucca.

Many authorities believe that floral structures and specialized mouth parts have arisen by reciprocal selection. This theory implies that plants and insects which show the greatest reciprocal specialization have the most descendants, while those having generalized forms are submerged in the struggle for existence. However, this theory, although logical, is not practical for there are many facts which discredits it.

Many floral structures, such as the forms and markings of the corolla, and the position of the various organs, have no known advantage which should make for continuence of the species. Many specialized flowers, e.g., the Orchids, are fast becoming extinct because of "over-adaptation" while such plants as the grasses, though possessing generalized flowers, are dominant and widely spread.

Another factor, perhaps the most important, is that flowers have probably played a comparatively small part in determining the success of plant groups. Even in the Compositae, the flowers owe

their advantage, not so much to the floral structures, as to the massing of inconspicuous flowers into a compact head.

There is another theory offered to solve this problem, that of orthogenesis. This theory states that both insects and flowers are not adapted to each other, but that insects in their visits to flowers select those whose structures are suited to their mouth parts. But this theory does not explain the cause of floral structures.

The evolution of the Orchids, the success of the groups with generalized flowers, and the probably dominance of the vegetative over the reproductive factors in many plants, all indicates that some other factor than natural selection has determined the diversity of floral structures.

It is quite evident that our present knowledge is inadequate to determine the evolution of floral structures.

The Symmetry of Flowers -

An examination of flowers from the standpoint of symmetry is necessary for the proper conception of floral mechanism. The time of anther-dehiscence or receptiveness of stigma maybe given a prominent place in a consideration of symmetry, but from a developmental standpoint all stages in the development of a flower as a mechanism are important.

Zygomorphic flowers are those in which there is a definite tendency in any member of a cycle of floral parts to reach a developmental stage in advance of the remaining members, or to

have the attainment of any developmental stage delayed.

An illustration of the development of zygomorphy may be found in Greyia sutherlandii. In this flower it is progressive, appearing first in the perianth, and later in the androecium and gynoecium. When the stamen-filament reaches its maximum length the anthers dehisce. The zygomorphy of the stamens is due to differences of filament-length which is due to an elongation of the filament-cells. The antero-posterior zygomorphy in the young bud is caused by differences in the cambial activity in the filaments while the later lateral zygomorphy is mainly due to differences in the rate of cell-elongation.

The relationships of symmetry of the several flowers to one another and the subordination of the symmetry of the individual flower to that of the whole inflorescence have not attracted attention till now.

In dorsiventral flowers there are two factors: either (1) the flowers are laid down radially and become dorsiventral in the course of their development; or (2) they are dorsiventral from the beginning.

Most dorsiventral flowers begin as radial structures and later become dorsiventral, the period varying from the unfolding of the flower-bud up to the open flower.

In the second category where dorsiventrality is brought about before unfolding we may distinquish two groups, according to their physiological relationships:

(a) those which are "essentially zygomorphous," as their deposition is always of a definite kind. The dorsal side of the flower is turned upwards, its ventral side downwards. The entrance is directed away from the axis of the inflorescence, a position which favors the visits of insects.

(b) on the other hand, the "unessentially zygomorphous" flowers are those which stand on the margin of the inflorescences. They become dorsiventral because the outwardly directed portion of the corolla is more strongly developed than is the inner.

In the former the dorsiventrality comes about either through the different construction of the parts of the flower which are laid down in different number or with a different construction from the outer parts. The relationships of symmetry of the several whorls of a flower do not change independently one of the other. In the latter, the change of symmetry is brought about chiefly by the reduction in the number of carpels. Many striking changes of symmetry are observed in the construction of the flower-envelope, especially the corolla.

Christian Konrad Sprengel was the first to establish the explanation of the structures of the flowers, why they are regular (radial) or irregular (dorsiventral). "As in so many other things, there are three circumstances out of which one can find an explanation of the structure of flowers, and of why they are regular or irregular. The first is the infloreseence, that is to say, the method in which the flowers are arranged on the stem branches of a plant. The second is, that the raindrops, at least

when the air is calm, fall perpendicularly upon the flowers. The third is the intention of nature that the flowers should be fertilized by insects, whether flying or moving otherwise, generally maintain an erect position."*

There are many advantages which spring from dorsiventrality. The zygomorphous structure of the flower allures agents for crossing and also excludes useless robbers of the honey, more seeds are produced by crossing and the plants are more vigorous as a result. Thus the need of adaptation to crossing can be easily seen. Darwin recognized the importance of zygomorphy for he says, "there is supreme dominating power of insects on the structure of flowers which is shown by the varied forms developed in consequence."*

" Sprengel, Das entdecke Geheimnis der Natur, Berlin 1793-p. 37
* Darwin -"Forms of Flowers" page 97

Summary of the Flower -

- Parts of the Flower
  - Floral Envelopes
    - Calyx, made up of sepals
    - Corolla, made up of petals
  - Essential parts
    - Stamens
      - Filament or stalk
      - Anther (with locules which contain pollen)
    - Pistils
      - Ovary
      - Style
      - Stigma
    - Simple pistil = 1 carpel
    - Compound " = 2 or more carpels

- Kind of Flowers
  - Complete flowers all four series of parts are present.
  - Incomplete flowers when one or more parts are absent.
  - Apetalous flower petals absent.
  - Naked flower both floral envelopes absent.
  - Perfect flowers stamens and pistils both present.
  - Imperfect flower
    - Staminate-stamens present, pistils absent.
    - Pistillate-pistils present, stamens absent.
  - Neutral or sterile flowers, stamens and pistils present in both or rudimentary.

- Form of Flowers
  - Regular, all parts of a set of the same shape or size.
  - Irregular, some parts of a set of a different shape or size.

- Flower parts all free
  - Flowers hypogynous
  - Calyx polysepalous
  - Carolla polypetalous

- Union of flower parts
  - Stamens united
    - Monadelphous - in one group
    - Diadelphous - in two groups
  - Carpels united — Compound pistil
  - Placentation of compound pistil
    - One locale
      - 2 or more parietal placentae
      - Free central placentae
    - Two or more locules-2 or more axile placentae
  - Stamens and petals borne on the calyxtube-perigynous
  - Calyx joined to the ovary, ovary is inferior.

- Flower clusters
  - Corymbose flower clusters (Indeterminate inflorescence)
    - Raceme
    - Panicle
    - Thyrsus
    - Corymb
    - Umbel
    - Spike
    - Head
    - Spadix
    - Catkin
  - Cymose flower clusters (Determinate flowers)
    - Helicoid cyme
    - Scorpioid cyme

REPRODUCTIVE ORGANS

The Stamens -

Development -

Stamens arise as homogeneous, small-celled tissue from their points of insertion on the stem. With later development a club-shaped form results, with the enlarged end, the anther, rapidly increasing in size, showing longitudinal grooves arranged in pairs. The cells of the anthers become separated into two tissues. The outside three layers of cells give rise to the wall of the anther. Within these tissues are large cells which form the archesporium. Upon developing, the archesporial cells divide, giving origin to the pollen mother-cells. The protoplasm within these cells divides, and each one becomes invested with a wall, thick and stratified. These are the pollen grains. In the conifers and cycads, there is a further division of the pollen, although only one of the cells takes actual part in fertilization.

The majority of flowers contain stamens arranged spirally or in whorls in the floral axis, few flowers possessing only a single stamen. The aggregate of stamens in a flower is called the Androecium. They are usually inserted between the leaves of the perianth and the carpels.

Structure -

The stamen is divided into two distinct parts, the anther, which produces the pollen, and its stalk, the filament. There is a great deal of evidence to prove that all petals originated from stamens, for the stamens in many flowers are partly metamorphosed into petals.

The parts of the anther which produce pollen are known as pollen-sacs; the tissue which bends these together is called the connective. There are a great many ways in which pollen adheres to the anther. If the walls of the mother-cells become absorbed, the pollen-sacs are filled with isolated cells. This condition is called free pollen. Pollen may adhere in clusters because of its sticky coat. Some grains remain as they arose in the mother-cells, united in fours, termed tetrads.

Many variations in the form of the anther are due to the relative dimensions of connective and pollen-sacs. The connective maybe broad as in the majority of Ranunculaceae, Magnoliaceae, and Nymphaeaceae, bar-shaped as in certain species of Salvia or reduced as in Mirabilis jalapa etc. The pollen-sacs range from globular to egg-shaped, and egg-shaped to linear.

Pollen is sometimes arranged in masses called pollinia. This mass of pollen is produced by a single archesporium, but differently arranged. In the Mimoseae, they are egg-shaped, or globular in form; in the Asclepiads, they are spatulate; in the Orchids, the pollinia terminates in a stalk which is attached at its other end to a disc.

Dehiscence of the Anthers -

When the pollen is ready to leave its place of origin, its cells become free from the inclosing wall of the anther, and lie embedded in the cavity of the pollen-sac until their release. The pollen-sac now opens and the pollen is liberated. This is called dehiscence. The parti-walls between each pair of sacs in the anthers breaks down and merge into two cavities which are called anther-halves.

Dehiscence is accomplished sometimes by the formation of holes or pores, sometimes by slits. In the Heath tribe and Pyrolaceae, the anthers dehisce by the former method. The pollen-sacs may be drawn out into tubes with an opening at their extremity, as in the Cowberry, Cranberry, and Wintergreen. The most frequent dehiscence is by slits which may be longitudinal or transerse, or sinuous or semicircular. The longitudinal slits reach from end to end of the pollen-sacs, or they may form short gaping clefts near the free extremity of the anther. The latter may be illustrated in the fig where the slits resemble pores. Although transverse slits are rare, examples may be found in a few Rosaceae, in Glabularia and Malva. Valvate dehiscence is very rare. Semicircular slits arise in the anther-wall, producing valves or trapdoors, as in Berberidaceae and Rauraceae.

Only in Ricinus is the pollen shaken out due to the mechanism of the anther. In this group the exothecial cells are thickened differently near the future opening and on the opposite side of the anthers. In the opening the walls are spirally

and annularly thickened, and tend to resist the opening movement of the opposite side. When dehiscence occurs the resistance is suddenly released and the walls fly back, throwing out the pollen. In the other cases the ejection is not connected with the opening of the anther, but is due to a tension in the filament, as in Parietaria officinalis. The elastic filaments are held by the anthers. At a certain stage of the opening of the male flower, the anthers come free with a jerk, then fly back, and the pollen is ejected.

In Zannichellia, there is a swelling of the inner cells of the wall which bursts the epiderm open. The endothecium consists of a layer of cells with their long axis at right angles to the surface of the anther wall, the inner wall being very thick. As the cells dry the cohesion of the diminishing water tends to cause the cells to collapse. The outer surface shrinks more than the inner, thus causing the anther to split, ejecting the pollen.

When the anthers dehisce, the two anther-halves partly separate from their attachments and become twisted or diverge at right angles. In Concolculus, Gentiana, and Menyanetres the anther-halves separate at the base only, the anther taking the form of an arrow-head. In the grasses they both separate and become somewhat bent forming an X-shaped anther, etc.

The various occurrences which accompany or succeed dehiscence depends upon some structual character of the anther-wall. In porous dehiscence the pores arise from the absorption of limited

portions of the wall. Where slits with movable lips or valves are developed, cells of characteristic structure are present, called contractile cells. By unequal thickening these cells cause the slit-margins to fold back or the valves to be raised.

There are a variety of methods by which pollen is discharged from the opened anthers. The filament may uncoil like a spring when the anther dehisces, as in the Nettle and Mulberry. In other plants the pollen is stored and slowly escapes, for example, in the Violet, it is stored in the grooves of the lowest petal; in Composites, the pollen is stored on the style or stigma and in the catkins of the Walnut, Hazel and Birch, the pollen is received upon the flowers below. A unique method is found in Sarracenia for here the pollen falls upon the stigma, which is in the form of an expanded umbrella. Kerner writes that there are over 20,000 species of plants which temporarily store its pollen in some portion of the flower.

The most frequent way is for the pollen to remain within the opened anther where it is disturbed by visiting insects.

Anthers are correlated with insect-visits. Where the slits or pores are directed towards the periphery of the flower, the anthers are extrorse, where toward the center of the flower, introrse. The anthers are extrorse in flowers having the honey situated outside the whorl of stamens, while they are introrse in flowers when the honey is between the ovary and the basis of the stamens.

The Pistil -

Structure -

The pistil consists of three parts, the ovary, the style, and the stigma. Just as the stamen assumes different forms according as its filament is long or short, its connective with or without appendage, its anther-lobes globular or oval, pear-shaped or linear, etc., so the form of the pistil varies in accordance with analogous diversities in the ovary, style, and stigma. The style may have its origin in the top of the ovary, when it is terminal; or from the side, when it is lateral; or from the base of the ovary, when it is basilar. Sometimes the style is absent, the stigma resting on the ovary. The term sessile is used to describe this condition.

Position of the Pistil -

The position of the pistil is important. The ovary may be superior, as in the geranium, where the other floral organs are attached to or below its base. In the apple and rose, there is a more vigorous growth of the axes by which a tube is formed around the carpels; the stamens and perianth are raised so that they stand on the apex of the rim of the tube. The term perigynous is used to describe this type of structure. In the begonia we have an illustration of a third mode of insertion where the ovaries are below the perianth, termed inferior.

The pistil or gynoecium the most persistent part of the flower.

as its office is to produce ovules, and after their fertilization to nourish them and protect them, together with the new germ that each may contain.

The structure of the gynoecium is made complicated by the fact that frequently the carpels are sunk into the tissues of the enlarged receptacle. This condition serves to protect and give more nutrition to the ovules as it brings them closer to the nutriment supply.

The Carpel -

The structure of the carpel is essentially a simplified foliage leaf; a vascular strand traverses each margin, where the ovules are found, this condition being called "marginal placentation." But in many cases the ovules are scattered over the inner surface of the carpellary wall, called "superficial placentation." Sometimes they are found on a prolongation of the axis in the ovarian cavity. This condition being called "free-central placentation."

The number and position of the constituent carpels is indicated by the stigmatic lobes. They are the readiest guide to the composition of the gynoecium.

The roughness of the stigmatic surface is due to the outgrowth of the superficial cells as papillae. The cells are thin-walled, with active protoplasts; frequently they are moist, or secrete a sticky juice, which helps to detain the pollen grains in contact with the surface.

The Style -

The style is often traversed by an open channel, so that direct access can be gained to the ovary from the stigma, e.g., in the Violet and Mignonette. In the Lily the channel is narrow and is filled with a mass of mucilage derived from epithelial cells which cover its surface. In other cases there is no actual canal, but a column of lax tissue with mucilaginous walls traverses the style, which serves as a conducting tissue, e.g., in Salvia and in the Mallow.

The Ovule -

The ovule, when mature, is more or less oval in form and is situated on a stalk, the funiculus. The central body of the ovule, the nucellus, is invested by one or two integuments which are attached to its base. These coverings closely cover it, leaving only a very narrow channel open at the apex, called the micropyle. The end which is attached to the funiculus is called the chalaza. The integuments and funiculus are accessory structures which provide respectively for external protection, and attachment with conduction of supplies.

When the ovule is mature the nucellus consists of a peripheral covering of thin-walled cells, of varying thickness, enclosing one large cavity, which, though its contents are complex is developed from a single cell. This is the embryo-sac or megaspore. The sac is limited by a very thin cell-wall which is

lined by dense granular protoplasm. Within this sac are seven nuceli, one of which is found in the center, and is of great size. There are two groups of three cells each, one fixed at the micropylar end, the other at chalazel end. The latter are often large, with well-marked nuclei, each of which is surrounded by an area of granular cytoplasm. This group is called the antipodal group as it occupies the base of the embryo-sac. At the micropylar end is another group of three cells, called the egg-apparatus. One of the cells projects further into the cavity and is called the ovum or egg-cell. The other two are known as the synergidae.

The cavity of the embryo-sac is filled by vacuolated cytoplasm, while in the center a large fusion-nucleus with a promiment nucleolus is suspended by cytoplasmic threads.

Though ovules may differ in form, in complexity of structure, in number of integuments, and even in number of their embryo-sacs, there is a marked consistency in the number and position of the bodies contained in the embryo-sac at the time of fertilization.*

The Disposition of the Stamens & Pistils -

The relative position of stamens and pistils is a matter of great importance in the process of pollination. The arrangement by which stamens and pistils occur in different flowers is termed declinism. Declinic species, plants possessing both staminate

*From "Botany of the Living Plant" - F.O.Bower - Page 378

and pistillate flowers, are monoecious if they occur on the same plant, and dioecious if the staminate and pistillate flowers grow on different plants.

In monoclinic or perfect flowers the rule is for stamens and stigmas to mature at different times, the condition being called dichogamy. Dichogamous flowers are protanderous when the anthers shed their pollen before the stigma is receptive, and protogynous when the stigma matures first.

POLLEN

Structure of pollen -

To the unaided vision, the pollen resembles so much dust, varying in color. On microscopic examination, however, each grain is seen to be a highly complicated structure. In general, the wall of the pollen grain is composed of three layers. These are the interior or intine, the middle or extine, and the external or perine. In the center of the grain is a tiny spot of protoplasmic matter which makes the pollen effective as a fertilizer.

In form, pollen grains are generally ellipsoidal, although many are angular or crystalline; others are narrow and lance-shaped. The pollen of the Pine possesses two bladders, resembling an insects head with two huge eyes. In *Tricopteris brachypteris* and *Basella alba* the grain is cubical in form.

In the case of most pollen grains, it is the outermost layer which attracts attention. This is not always of the same thickness in every part, thin places here and there resembling actual openings. At certain points on the surface, disfiguring outgrowths arise. These are surmounted by small cap-like structures. When the time comes for the emerging of the pollen tube from the grain, one of these caps is detached which enables the tube to grow outward and to plunge down the tissue of the style to the ovule.

The majority of grains are variously striated and grooved. In ellipsoidal and spherical grains, the grooves run like meridian-lines. It is remarkable to note that the number of grooves is constant for a given species, and even for whole families of plants.

Some pollen grains are covered with a sticky substance called viscin. On the slightest touch the substance can be drawn out into delicate threads. This substance is probably a mucilage formed from the outer wall of the pollen-tetrad, or broken down walls of the mother-cells.

Pollen grains swell up rapidly when placed in water. The thin places in the wall allows the inner protoplasm to swell and stretch. The grooves in the grain become inflated, and the grains occupy a much larger space. Finally the thin spots are ruptured, and the protoplasm leaves the extine. It is advantageous for the young pollen-tube, as it leaves the extine that the coat should be fixed firmly; for this purpose, the various ridges, teeth, and spines on the surface serve as a means of anchoring the pollen-grain, while the pollen-tube is being formed.

However, the most important feature of the sculpturing on the surface of the pollen-grain is the ability of the grain to adhere to the splits of opened anthers and become attached to insects and other animals.

Besides this clinging pollen is the dusty pollen with smooth and non-adhesive surface which is carried away with the slightest breeze. Globular or ellipsoidal grains with smooth surfaces are

saturated with oil.

The crystalline forms, the various sculpturings, spines, and other projections, as well as the presence of oil and viscin on the surface of the pollen-grain are arrangements by which the adhesiveness of the grains is increased.

The submersion of pollen in water produces an instantaneous absorption of water resulting in the swelling of the pollen-cell. However, no real growth can take place in a short time. What has happened is really an expansion of the intine and a smoothing out of the folds in the walls. Sometimes the limits of elasticity are exceeded and part of the intine gives way, allowing the spermataplasm to escape. If this happens the pollen cell is destroyed. Even if this does not happen the protoplasm loses the power of fertilization through the rapid absorption of water, thus the pollen-cells are literally drowned.

Protection of pollen-

Pollen grains are exposed to a great many risks, either in transit, as food for insects, or injury from weather. To overcome this loss, pollen is produced in large quantities and the number of stamens is increased. In many trees the great loss of pollen is offset by the development of a large number of flowers, especially imperfect ones. In the grasses and sedges, the amount of pollen is small but densely associated through the whole group before it is blown away.

In order to preserve the pollen against the injurious effects

of moisture, protective apparatus must be developed.

By structure -

There are many methods by which flowers protect their pollen. The flowers of the Heather have bell or cup-shaped corollas which hang down from curved stalks with the opening of the flowers toward the earth, and so cover the anthers.

The means of protection are diversified according to whether it shelters the new-opened anthers or that part of the flower whereon pollen liberated from the anthers is temporarily deposited; they also vary according as it is the anther-walls, stigmas, petals, involucre, or foliage leaves which serve as a roof to the pollen. The lime-tree has its pollen protected by the broad, flat, foliage-leaves. In Impatiens, the flower-buds are held by delicate stalks above the surfaces of the leaves from whose axils they come, and the leaves fold upward like troughs. The leaf later flattens out and when the anthers open, they are rubbed by a smooth lamina, off which the rain falls.

Several of the Arvidae have the spadix completely covered by large involucral sheaths which dry up and drop off after the pollen has all been removed.

In the dioecious Sea-Buckthorn, Hippophae rhamnoides, which is arranged in spikes, the four anthers seated in the axils of scaly bracts at the bases of the young lateral shoots in each flower, discharge their powdery pollen while the flower is closed. The orange pollen is stored in the bottom of the flower

awaiting a dry wind to transport it. To protect it while it is in storage a pair of curved perianth leaves turn inwards thus forming a bladder which incloses the anthers. The two parts dehisce at the sides and the top forms an arch which completely shelters, the mass of pollen which is later removed through these slits by the wind.

Plants of the globe flower, Troelius, grow in the arctic regions in damp situations. The pollen is protected by the anthers being completely shut in by the perianth leaves, spirally inserted on the receptacle and closely furled one upon another.

In Toad Flax and Snap-dragon, the corolla forms a closed envelope round the anthers, thus the pollen is hidden in the cavity formed by the two petals of the keel.

The pollen is protected by an arched portion of the flower which forms a roof over it in Butterwort, Cow-wheat, and Yellow-rattle.

The flowers of Hydrangea quercifolia are of two kinds, each growing in large bunches. One group includes flowers having pistils and stamens with a small, greenish perianth not able to protect the pollen; the other group has neither stamens nor pistils but possess large sepals which act like an umbrella. The latter are found on the outermost and uppermost branches of the inflor-escence and are always in a position to protect the pollen of the pollen-bearing flowers which are underneath, from being wet by the rain.

Hypocrateriform flowers have a still different method.

The tubular part of the c orolla expands into a limb, on which the rain or dew collects. The opening where the tube passes into the limb of the corolla is so contracted that even the air cannot escape from the tube. Phlox and Daphne belong to this group.

In the group of structurally protected pollen belong all flowers in which protection results from the structure or shape of the flower, of the flower parts, or of the flower cluster.

There may be protection from the structure of the grain itself or from the form of the stamen, pistil, corolla, calyx, bract, or inflorescence. The pollen grain has a great deal of protection in its thick wall, often increased by oil or viscin, as in Onagra, Circoea, etc., There may be protection in the position of the anther, or the location of the pore by which it opens. The swelling in the staminate scales of the conifers closes the way to the pollen grains. The shape of the corolla provides a means of protection, illustrated in the Gentiana, Lithospernum, etc. The form of the spathe, as in Arisaema and Araceoe, serves as a protection. There are large bracts in some catkin-bearers which afford shelters.

As moisture causes the premature germination in some plants and ruins the possibility of fertilization in the majority of plants, the need of protection of the pollen can be easily noted.

By Movement -

There is a long list of flowers that have their pollen protected by various movements of the parts of the flower itself.

This movement is evident in those flowers having their pollen exposed to the rain.

Although the habit of opening and closing during day and night was probably developed in relation to insects, this movement also protects the pollen. Petals which close over the anther in the evening grow very large in the flowering period as in some Ranunculaceae. In the water-lily (Nymphaea) the petals close when the dew falls and in damp weather do not open at all.

In plants with funnel-shaped, tubular, or bowl-shaped corollas the folding is complex for there must be a bending and twisting of the petals before the flower is completely closed.

In apetalous flowers sometimes the sepal closes, this also gives protection to the pollen. In many geraniums, umbellifers, and composites, the entire flower cluster droops. There is also an upward or inward movement of the ligules in ligulate and certain radiate flowers.

These movements of the various parts of the flower are due to alterations in the tensions of the layers of tissue involved as a result of variations in heat and light and partly to the fluctuation in the degree of moisture.

In the Carline thistle (Carlina acaulis) the opening and closing depends entirely on the moisture in the air. When the air is warm and dry, the rays are outwardly curved and are spread widely. With the slightest increase in moisture, the rays bend inward and form a compact tent around the anthers.

Alterations in the form and position of certain tissue of the stamens affords protection in the plane trees, conifers, yews, and junipers. The pollen-cases are borne on peltate stalks, and are attached like scales of a fir-cone, on the inner surface of which the pollen is developed. Where there is a great deal of moisture the scales absorb it and swell until their edges are in contact with each other, thus protecting the pollen within.

In many flowers the protection is afforded by simply bending the stalks and stem which converts cup-shaped flowers into pendulous bells. The stalks of the Lily of the Valley bend just enough to incline the mouths of the flowers in a lateral direction.

Flowers of the South African Sparmanmia are borne in umbels. The stalks are curved outwards and downwards away from the main axis so that the flowers are inverted and their anthers are turned towards the ground and covered over by the petals. As the margins of the petals overlap, the flower forms a basin open to the sky. This basin fills with water and with increased strain, tips over, letting the water run out without wetting the cluster of stamens suspended beneath it.

In Plantago and Glabularia the anthers are borne on long filaments which project out beyond the flower. If wet weather occurs the anthers close up and encase the pollen. This movement of the anthers is due to the moisture in the air which causes a contraction and expansion of the hygroscopic cells underneath the epidermis of the anther-walls.

The inflection and straightening of the flowering axis and the inferior ovaries are brought about in the same way as the periodic movements of petals and bracts, that is, by alternations in the tensions of the tissues. These variations intensions are due partly to vicissitudes in respect of heat and light, and of the degree of moisture in the air.

In flowers where the petals and anthers open and close, the movements are simultaneously. In the Bulbocodium the cause of the movement of petals and anthers is different. After a long rain, the petals open under the influence of the sun but the anthers remain closed due to the excessive moisture of the atmosphere.

The closing of the anthers in the Bastard toad-flax, Thesium alpinum, is effected by peculiar tufts of hair projecting from the perianth. Moist weather does not affect the position of the flower-stalks. The perianth-lobes of the flowers are connected with the anthers standing in front of them by a tuft of twisted hairs, susceptible to wetting, which conduct the water to the anthers, thus causing them to close.

In several composites, e.g., Onopordon and Centaurea, the pollen is conveyed to the mouth of the tube by the contraction of the filiform which supports the anther-cylinder. These filaments with mechanical stimuli contract and pull down the pollen tube. Thus the style which was inside of the tube is exposed. A mechanical stimulation caused by the touch of the legs or proboscces causes the contraction of the filament, the

retraction of the anther-tube, and the exposure of the pollen. Before this stimulation the pollen is hidden in a sheath formed by the anthers.

Frequently, plants have two or three devices for protecting pollen in case one should fail. This condition is noticed chiefly in those plants having a small amount of pollen, where the flowers are small, where the time allowed for the flower to unfold is limited, and where the pollen is carried exclusively by flying insects.

METHODS OF POLLINATION

Autogamy -

Autogamy or self-pollination is the transference of pollen from the stamens to the stigmas of the same flower. This process only occurs in hermaphrodite flowers. Self-pollination is important and the contrivances which bring it about are no less numerous than those of cross-pollination.

Methods -

The simplest method of autogamy is found in flowers where, when the flower opens, the stigma is found in the front of the entrance to the receptacle and already mature. The anthers adjacent to the stigma open and cover it with pollen. This may be observed in a few varieties of annual plants with small flowers, and again in bulbous plants belonging to Lilifloreae.

In Sprinkling Flowers -

The anthers of pendent flowers are joined together in a cone. At the close of the flowering period there is a relaxation of the filaments. The slightest vibration of the blossom causes the pollen to be displaced, in consequence of which it falls to the receptive stigma below.

Even in upright flowers autogamy takes place. The pollen of these flowers slips down the smooth sloping wall of the funnel to the stigma, the carolla acting as a c onduct for the pollen.

In erect or oblique flowers, the elongation of the filaments produces autogamy. By this process the anthers are elevated to the level of the stigmas and are thus enabled to deposit their pollen upon them.

By Elongation of the Stamens -

In many protandous Caryophyllaceae, autogamy is brought about by the elongation of the stamens. There are various changes which take place in flowers of this kind. In many cases the stigmas are the agents in the transfer of pollen to themselves from the anthers of the same flower. They may be classified into two division: (1) those in which there is a direct contact between the anthers and stigmas by some movement of the pistil, and (2) those in which pollen is stored in the flower and then the stigma is brought into contact with it by various movements by the pistil. In the former autogamy is produced by a contraction of the style, while in the latter, by an elongation of the ovary or the style. The accomplishment by autogamy through the inclination of the style is only found in rare cases, e.g., in the bilabiate flowers of the North America species Collinsonia canadensis.

A much more common method is by the movement of the pistil, by bending so as to bring the stigmas in contact with the anthers, or in such a position beneath the anthers so that they can catch the falling pollen.

A rare method of autogamy is found in plants where the filaments and style coil in spirals and become entangled just before

the flower fades, placing the stigmas in contact with the pollen of the anthers, e.g., in a number of Commelynaceae.

By Movement of the Corolla -

The previous methods discussed have dealt only with the movements of stamens and pistils. But in flowers which are in the shape of tubes, cups, or basins, autogamy is brought about by the contraction or closing together of the corolla, e.g., in Thymelaea passeuna. In many plants as the corolla falls off, its tube slips over the stigma, so that the latter rubs against the anthers. This method presupposes that when the flower is in full bloom the anthers are overtopped by the stigma, and that the latter is still in a receptive condition at the time the corolla becomes detached and drops.

One of the most curious contrivances for effecting autogamy consists in a special inflection of the corolla enabling it to conduct the pollen which falls from the anthers to the stigma, e.g., in two species of the Lousewort belonging to the genus Pedicularis. In the last stage of blooming the filaments become flaccid, consequently the pollen falls upon the slit on the upper lip under the galeate arch of the flower. The lip undergoes a bending downward so that a tube is formed. The stigma, which is at the mouth of the tube, is in a position to receive the pollen.

By Movement of the Flower Stalks -

The accomplishment of autogamy by various com-

binations of movements and inflections of the flower stalks with similar action on the part of the stamens and style is a common occurrence in many plants. The hermaphrodite flowers of many Rosaceae afford examples of this type of autogamy. We may have (1) the inflection of the pedicels, (2) the elongation of the petals, (3) the elongation of the stamens, and (4) the inflection of the styles, coöperating towards the same end, namely, that in the event of no insects visiting a flower all the stigmas may receive pollen from the anthers developed in the flower itself.

It is evident that there are numerous contrivances whereby autogamy is promoted in hermaphodite flowers, though any mechanism which leads to autogamy has full scope for its operation only if cross-fertilization has not been previously effected.

Prevention of Autogamy -

In many plants Sprengel had observed that the two sets of sexual organs in the same flower are not developed simultaneously; to this phenomenon he gave the name dichogamy. In his introduction he says: "Since very many flowers are of one sex only, and probably as many more are dichogamous, nature seems to intend that no flower shall be fertilised by means of its own pollen,"* and as a proof of this he adduces an experiment performed by him on Hemerocallis fulva, which showed him that this plant is not fertile to its own pollen.

* Conrad Sprengel - Das entdeckte Geheimniss der Natur im Bauc und in der Befruchtung der Blumen (Berlin--1793) page 43.

Dichogamy -

The commonest feature in flowers that makes close fertilization difficult is dichogamy, that is, the consecutive maturity of anthers and stigmas. Dichogamous flowers are either proterandrous, as when the pollen escapes from the anthers before the stigma in the same flower is ready for pollination, or proterogynous, as when the stigma has lost its capacity for pollination before the pollen is mature, so that its pollination must depend on the pollen of older flowers. Most species of Geranium, Malva, Umbelliferal, and Compositae, are proterandrous; while among proterogynous plants may be mentioned species of Magnolia, Aristolochia, and Plantago.

Mechanical Features -

In many Lilies and Evening Primroses the stigma projects beyond the anthers so that the pollen cannot fall upon the stigma of the same flower. The receptive surface of the stigma in many flowers is so arranged that the insect brushes against it upon entering but not upon leaving the flower. Close-pollination is prevented in flowers with extrorse anthers and also in pendulous flowers where the stamens would have to project beyond the stigma.

Heterostyly -

Another condition, called heterostyly, hinders close pollination by having the stigmas and the anthers in

different flowers occupying different positions. In Primula acaulis the five stamens are halfway down the throat of the corolla. A long style carries the stigma to the mouth. In other plants the stamens are at the mouth with a short style about halfway up the tube. As a result, the visiting insects transfer the pollen from the long-styled flowers to the short-styled flowers.

Self-Sterility -

The most perfect method by which autogamy is prevented may be illustrated in flowers in which the pollen is sterile. Even when the pollen is not exactly self-sterile, the pollen of another plant grows tubes quicker than its own. This differential growth rate in pollen tubes may be found in Pumex and Lychnis. A cause of self-sterility in pollen is its failure to germinate. The actual cause of this failure is not known. Correus believes that it is due to the presence of an inhibiting agent, e.g., in the Orchids. Jost, however, believes the failure is due to the lack of some essential growth factor. He points out to prove this statement that a pollen tube never attains its normal length in a culture solution. Compton (1913) compares the inhibition of the pollen tube growth and the phenomena of immunity to disease in the animal kingdom. Possibly in the cells of the stigma there is an anti-body which inhibits further growth, formed as a reaction to the entrance of the pollen tube.

Summary -

A. Male and female organs in different flowers (diclinism).
Cross-fertilization ensured, and effected by insects or by the wind. Ex. Cannabis.

B. Male and female organs in one and the same flower (monoclinism).

1. The organs of the two sexes not developed simultaneously (dichogamy).
   - (a) The male before the female. Ex. Geranium pratense.
   - (b) The female before the male. Ex. Luzula pilosa.
     Self-fertilization usually prevented, and cross-fertilization effected by insects.
2. The organs of both sexes developed simultaneously (homogamy).
   - (a) Flowers expanding (flores chasmogami, Axell).
     - 1. Anthers distant from the stigma.
       - a. Styles of different lengths on different plants of the same species (Heterostyly, Hild.; dimorphism and trimorphism, Darwin).
         Self-fertilization not altogether prevented, but either quite inoperative (Pulmonaria officinalis) or yielding little result (Primula sinensis).
       - b. Styles of the same length in all the flowers (Homostyly).
         Reproductive organs changing their relative positions during the flowering period.
         Self-fertilization avoided, cross-fertilization effected by insects. Ex. Anoda hastata.
         Reproductive organs remain unchanged in position during the flowering period.
         The aid of insects necessary for fertilization.
         Self-fertilization to a great extent impossible, and cross-fertilization necessary. Ex. Orchidaceoe.
         Self-fertilization to a certain extent possible, but not necessary; cross-fertilization more probable. Ex. Asclepiadew.
         The aid of insects not essential.
         Self-fertilization possible, but cross-fertilization also effected by insects.
     - 11. Anthers lying close to the stigma; self-fertilization inevitable.
       No seed produced without cross-fertilization, which is effected by insects. Ex. Corydalis cava.
       Seed is produced on self-fertilization, but cross-fertilization by insects is not excluded.
   - (b) The flowers never expand (flores cleistogami, Kuhn).
     Only self-fertilization occurs, and all cross-fertilization is excluded; but the plants have other flowers which open and are liable to cross-fertilization. Ex. Oxalis acetosella.*

* H. Mueller - "The Fertilization of Flowers"--Pages 12-13

Geitonogamy -

Geitonogamy (from γείτων, a neighbor and γάμος, marriage) is the crossing of pollen from one flower to another on the same plant. The transportation being effected both by wind and by flower-visiting insects.

Geitonogamy may be direct or indirect. In the former, as in most cleistogamous flowers, the contiguity of stamens and pistils, or the position of the stamen above the pistil, permits the pollen to fall directly upon the stigma. In the latter, the transfer of pollen is the result of the growth or movement of the various organs of the flower, which may include movements of stamens or style, their elongation or contraction the closing of the perianth, or the falling of the corolla. However, it may be brought about by the pressing of mature stigmas on the liberated pollen of neighboring flowers or by the actual falling of pollen upon them.

Where the flowers are crowded together, as in umbels, bunches, spikes, etc., the stigmas of one flower can easily reach the pollen-covered anthers of another. This particular form of crossing occurs frequently in Compositae.

In Compositae, e.g., in Prenanthes, having only "ray" or ligulate florets, the long thin style is inclosed in a tube of anther enclosed in each floret. The style is covered with stiff bristles and as it elongates, after the opening of the flower, these hairs sweep out the pollen which has been already shed into the interior of the anther-tube. The two branches of the style,

now projecting from the empty tube of anthers, soon separate and twist sideways and downwards. At the same time adjacent styles come nearer to one another and in this way the stigmas come in contact with each other, and pollination ensues.

In the Salsify, as in many other plants, geitonogamy is assisted by the arrangement of the flowers in each capitulum. Each flower of the outer row is placed exactly between two of the inner row. Thus when the capitulum closes, the two curved style branches of the outer row become applied to the pollen-covered styles of the inner flowers.

Among umbelliferous plants, the numerous small flowers are crowded so closely together that the stigmas and pollen of neighboring flowers can easily touch.

In the genera Eryngium and Hacquetea, the flowers are crowded together in capitalate masses surrounded by broad bracts. The stamens are bent inwards in each flower and the petals still unfolded, but with sticky stigma projecting from the bud. Later the filaments elongate, the anthers dehisce, and the styles are so inclined that the stigmas are placed in a position so they are brushed against the pollen-covered anthers of neighboring flowers.

One of the most remarkable cases of geitonogamy may be observed in Beaked Parsley Fermel or Water Parsnip. There are two kinds of inflorescence. The umbels which blossom first contain the hermaphrodite flowers; the later umbels consist only of staminate flowers. In the hermaphrodite flowers, the anthers

borne on very thin filaments, are brought to the center of the flower, where they dehisce and scatter their pollen. After the five stamens have dropped off, the stigmas become mature and receptive. In two or three days the pedicels of the staminate flowers elongate. When the anthers open the pollen falls vertically downward into the stigmas of the lower flowers. It is easy to see that the majority of the stigmas are pollinated in this manner.

In Eupatorium aromaticum and cannabimin the styles are divided into two long threadlike branches which bear stigmatic tissues on their lower portions. During the elongation of the styles, which are studded with short bristles, some pollen is brushed from the anther-tube, which adheres to the each branch of the style. Later the style branches, exposing the receptive stigmatic surfaces, which, with the adherent pollen, commonly come into contact with the divergent branches of older neighboring florets.

The illustrations of geitonogamy described in Compositae and Umbelliferae may be regarded as typical of what occurs in may representatives of other families. For example in Rubiaceae, Caprifoliaceae, Cornaceae, Rosaceae, and Arvideae, where the flowers are crowded together in balls, fascicles, spikes, or racemes. In Snake root and in Calla palustris the flowers are crowded together in short spikes. The stigma in the lower inflorescence does not ripen until the flowers are shedding their pollen. This feature resembles the fall of pollen in Compositae.

In the racemes of Eremurus, the stigmas at the end of the straightened style are brought, by their change of position, directly into contact with the pollen clinging to the anthers of the higher flowers. The stigmas are always mature when the perianth opens.

The flowers of the rhubarb are protandrous. The anthers which project above the perianth, open and emit their pollen. At the same time the three styles on the top of the ovary are bent back. The pollen does not reach the stigmas because they are hidden at the base of the perianth. The styles straighten when all the anthers have fallen off. Thus the pollen from the anthers of the younger flowers usually falls on the stigmas, which do not emerge, but become conspicuous by the folding back of the perianth leaves, and are thus rendered accessible to the pollen of neighboring flowers.

In many plants e.g., the Ericaceae, geitonogamy is accomplished by visiting insects. The Mediterranean Heath may be taken as an illustration. As the stigmas protrude some distance from the corolla, the bees inevitably brush them when they come to suck the honey at the base of the flower. The anthers are disturbed by the bee, with a result that the bee becomes powdered with pollen. This pollen is deposited when the bee visits another flower. In the Toothwort the fertilization is effected in a similar way. Humble bees suck the honey secreted below the ovary. In doing this it becomes covered with pollen which it transfers

from flower to flower as the insect usually visits all the flowers on a given plant before flying to another.

Geitonogamy is intermediate between xenogamy and autogamy. Although it is often classed with the former, in reality it resembles more the latter.

Cleistogamy -

Cleistogamous flowers are the culmination of structures which facilitate self-pollination. There are two types of flowers which never open, first, habitual, and second, those depending upon definite external factors. In Lamium the chief cause is subjection to low temperature, in Alisma the flowers are cleistogamous in the shade, indicating that light as well as heat may be a factor. In the subterranean flowers of Viola cucullata, Amphicarpaea, and Polygala polygama, habitual cleistogamy is well illustrated.

Goebel (1904) has shown that cleistogamous flowers have been inhibited in some stage of their development. These flowers correspond to an early development of the open flower, at this early stage, functional maturity of the germ cell is reached. The most general feature is the reduction of the corolla which either is lacking or exists in the form of protuberances. The stamens are few in number and usually the pollen grains are very much reduced in quantity. Occasionally the pistil exhibits reduction, e.g., in Helianthemum which only has a few ovules. On the whole there is a reduction of floral structures.

Many forms of cleistogamous flowers are subterranean, as in some species of Violets and the Milkwort. This type of pollination seems to be effected under many conditions. In general, as in the Balsams, the presence of a fungus has induced cleistogamy, and the same effect has been observed on Biscutetla when attacked by certain parasitic insects. Nutrition seems to be another factor,

as indicated by the fact that the touch-me-not, Impaties nole-tangere, which ordinarily produces both open and closed flowers, will produce only the latter when the plant is transported to a habitat providing poor nutrition. It has also been shown in the case of a certain species of Violets that the sun wields some influence; plants grown in the shade produce only cleistogamous flowers. Another factor, and perhaps the strongest, is the temperature, cool temperature inducing the production of self-fertilizing flowers.

XENOGAMY

Wind Pollination -

In the flowering land plants the simplest agency of pollination is the wind. This type of pollination occurs in most of our trees, for example, in the Elms, Birches, Oaks, Pines, and in such shrubs as the Alders. In these plants the smooth light pollen grains are often provided with bladders or wings, thereby presenting more surface to the wind. Moreover, they are produced in vast quantities to compensate for the inevitable waste of this method. For this reason the staminate flowers outnumber the pistillate, a circumstance illustrated by the fact that long hanging staminate catkins are familiar to everyone while the pistillate flowers, which commonly occur in separate blossoms, are so inconspicuous that they are very little known to the casual observer.

Efficiency -

It is obvious that the efficiency of wind pollination depends on the greatest possible freedom of wind action. This is the reason why so many wind-pollinated flowers open in the early spring before the leaves have appeared, as catkins, and the flowers of the Maples.

Not every aerial current is favorable to the dispersal of pollen. Some have rain deposits and the pollen is washed away where it perishes, while storms of wind forcibly whirl away the pollen. The best result is obtained by having the pollen

distributed uniformly over an ever-extending area, becoming diluted and forming a cloud of dimishing density, scattered over a wide area. This is occasioned by a gentle wind.

The forest trees distributing their pollen by the wind generally have their flowers clustered together in catkins. It is quite evident why wind-pollination is advantageous to the trees for their height makes it easy for the wind to move through them. Most catkins are long and are easily moved by the wind, having numerous flowers in each, they shake out enormous quantites of pollen.

Many plants dispersed by the wind, have dioecious or monoecious flowers. Those having hermaphrodite flowers show complete dichogamy, the androceium and gynoecium ripen at different times, the stigma being withered when the anthers scatter their pollen.

Several plants that are pollinated by the wind are dichogamous, that is, the stigmas in a receptive condition are situated higher than the anthers from which pollen is emitted. In the Plantain (Plantago) the styles with stigmas ready to receive the pollen, project from the uppermost flowers in each spike. The pollen, therefore, must travel upward.

Wind Pollination in the Trees -

In the Oak, Beech and Alder, the catkins of mature flowers hang down in the form of swinging tassels. The flowers with mature stigmas are above them. In the majority of cases the pollen dispersed by the wind soars upwards and either reaches the stigmas

on their way or later on, settle on the stigmas on their way down.

A good example of a wind-pollinated tree is the Hazel. The male flowers are grouped together to form a long catkin which are generally high up on the tree. Each blossom is covered with tiny brown scales arranged like tiles on a roof. There are about eight stamens to each blossom, with little trace of a calyx or corolla. The female flowers are grouped in queer little buds, well protected by scales. The red style and feathery stigma project above to catch the pollen.

In many wind pollinated plants the pollen is violently ejected from the anthers. This depends on the fact that the filaments bearing the anthers are coiled in the bud and suddenly spring up at the same moment that the dehiscence of the anthers take place. Ejection ensues only when a light, dry wind blows which causes an alteration in the tension of the tissues. If there is no wind, or the air is damp, pollen is not ejected. Thus the air liberates the pollen by either shaking the flower axis or affecting the tension of the tissues, thus freeing the pollen.

Wind-pollinated plants with short, thick filaments have anthers filled with pollen of a flowery consistency. The common Ash is an example of this type. The anthers are closed when they protrude beyond the inconspicuous floral envelope. Dehiscence is accomplished by longitudinal fissuring of the anther-lobes, each pair being transformed into an open recess. The loss of pollen is overcome by the fact that before dehiscence the anthers arrange themselves so that the fissure is turned upwards.

The Grasses -

The grasses have anthers borne on long filaments, the stigmas maturing before them. By a sudden distension of the bracts, due to a special turgid tissue at their base, the anthers are exposed beyond the glumes. Then the filaments increase in size by a rapid longitudinal growth. When the anther has assumed a pendent position the dehiscence commences. As the filament and anther are attached by a slender connective, the anther moves about freely. The anthers, which consist of two parallel lobes, open along the sutures with the two anther-lobes separating and curving around in the opposite direction. When the splits open the pollen falls into these upturned anther-ends and is thus prevented from being lost. After the pollen is blown away, the boats formed by the ends of the anthers are being continually refilled until the pollen is all gone. When the anthers are emptied they drop off in the form of dry husks.

The temperature and hygroscopic condition of the air plays a great part at the time of dehiscence. The most favorable time for the grasses is the early morning when there is some dew present, some sunshine, rising temperature, and a gentle breeze.

The opening of the glumes and the extrusion of the anthers are often connected with alterations in the position and inclination of the stalks. The pedicels of agrostis form an angle of from 45° to 80° from the axis during pollination. These movements are designated to give sufficient room to the anthers when they are

exserted, in order that they may move freely. When the flowers are close together the bracts do not spring open but merely relax. The filaments increase in length and are raised above the glumes.

In numerous species of Sorrel and Meadow-rue, the anthers are pendulous at the ends of filaments. Perianth-leaves form the protective envelope around the anthers before they open. In the Meadow-rue, the anther-lobes exhibit parallel slits which are very narrow. Plantains have their pollen dispersed from anthers borne on long filaments. When the petals unfold, the filaments straighten out and project beyond the floral spike.

Stored Pollen -

In many plants the pollen is not dispersed from the point of origin but from some spot within the flower where it is stored, being protected from the wet. Different parts of the flower are used for the halting places. In the Pines and Firs the backs of the polleniferous scales serve as a storing place. The upper surface of each anther-scale is slightly excavated, the lateral edges being reflexed and turned up forming a trough within which the pollen is stored. In the Yew, the connective in the anther- lobes terminates in a circular shield with a crenate margin. The anther-lobes are attached to the under side of this shield. When the pollen-sacs are mature they burst open, their walls shriveling. The shields now resemble cupolas supported by short columns, arching over the space containing the pollen. As

the tissues of the shield contract in a warm, dry atmosphere, chinks appear between the shields. With the action of the wind the pollen is blown out through these chinks. In damp weather the chinks lock together and the pollen is enclosed where it is protected from the wet. In the Junipers, Cypress, and Arbor Vitae the stamens have a peltate connective spread over the anthers, each stamen being short with a thick head; this connective keeps the edges of the stamens in contact. When individual stamens fall out, a gap is made by which the pollen escapes.

In the Hazel, Walnut, and Alder, there is a temporary deposition of the pollen on the backs of the flowers. The floral spikes are in the form of short, thick cones. These cones are erect at first but later become pendent and elongate just before the anthers burst. The back of each flower, which is now turned upwards, is contrived to catch the pollen from the anthers of the flowers above it..

In the curled pondweed, Potamogeton crispus, the flower-spikes appear above the surface of the water, in which the large, fleshy stigmas are mature and ready to receive the pollen about the middle of the summer. The perianth-leaves of the flowers are folded together beneath the four projecting stigmatic lobes, while the anthers are hidden beneath the perianth. When the stigmas wither the concave perianth-leaves open. At the same time there are longitudinal slits formed down the large anthers, out of which flows a large supply of pollen. If there isn't any wind to blow the pollen away, it drops into the perianth-leaf just

below the anthers. However, if there is a strong wind the pollen is carried away to nearby flowers where the four radiating stigmatic lobes are in a receptive condition.

Another striking example of an instance where the pollen is temporarily stored in concave perianth-leaves is found in the Arrow-grass. The stamens are in two whorls, three in each whorl, situated one above the other, while beneath each stamen there is a deeply-concave perianth-leaf. When the anther opens, the pollen rolls into the receptacle beneath it. All the six anthers do not open at once. The lower whorl opens first and when their pollen has been carried away, the empty stamens and perianth-leaves drop off. The same process is repeated with the other whorls.

A third example of this type may be found in the Sea-Buckthorn (Hippophae). Each male flower consists of four stamens, and two opposite concave scales. These scales form a bladder within which the stamens are concealed. The orange-yellow pollen is set free from the anthers while the bladder is still closed. The bladders open when there is a warm, dry wind blowing, while in damp weather, they close up quickly and protect the remaining pollen.

Adaptations -

There is a close connection between the various contrivances to ensure that pollination shall only take place at the best possible moment, and the maintenance of a free passage in

the direction in which the pollen is to be transported by the wind. There is also an adaptation between the above and the shape of the stigmas which receive the pollen. These adaptations may be noted by: (1) the flowers are arranged in spikes and panicles at the upper extremities of the shoots and project freely into the air, (2) the plants never have a mass of foliage, (3) a number of plants yield up their pollen when the green foliage is still folded or is just emerging, (4) some have no leaves at the time of pollination, as in the Alder, Ash, Elm, etc. and (5) the pollem is dusty and the stigmas are designed to catch the pollen.

It is very important that the pollen is produced in large quantities as the wind is but an uncertain means of transportation and incapable of exercising any influence on the selection of a route.

"The efficiency of anemophily is proven not only by its age, but also by the fact that if the number of individuals is considered rather than the number of species, then far more plants are pollinated to-day by wind than by insects."*

* Lovell -- The Flower and the Bee -- Page 46

SUMMARY OF WIND POLLINATION

1. The flowers, in general, are inconspicous, lacking colored corolla, odor, and nectar. Such prominence as they possess is due simply to their abundance, or to their colored anthers.

2. The stigmas are large, often branching; also feathery, thus spreading a greater net for the drifting pollen.

3. The male blossoms far exceed the female in number, a provision made because of the wastefulness of the method.

4. The flowers are borne in ways to insure free passage of the pollen without interference by leaves. Thus the flowers unfold before the foliage in the spring, as is the case with most of our trees, or else are lifted beyond or above the leaves, as in the pines and grasses.

5. The pollen is light in weight and exhibits large surfaces, even increased, as in the pines, by extension into large empty bladders.

6. The stamens and pistils are commonly borne in separate flowers, often upon different plants, thus preventing close-pollination.*

*Ganong -- Textbook of Botany -- Page 289

Water Pollination -

Perhaps one of the strangest and most interesting methods of securing cross-fertilization is that used by certain water plants which have their flower stalks entirely hidden under the water. Let us examine the Italian eel-grass, Vallisneria spiralis, as an illustration of this unique method of pollination.

The epigynous seed-bearing flowers of Vallisneria are borne singly, each within its spathe, at the end of a long scape, which anchors the floating flower to the short upright stem at the bottom of the pond. Through the elongation of this axis the spathe reaches the surface and opens at its outer end, but remains as a partial blocking of the ovary until the seeds are nearly mature. The three spoon-like sepals soon come apart, disclosing the three bifid stigmas, which are coiled in the center of the flower. These stigmas are seen to be densely clothed with stigmatic hairs, conspicuous because of their snowy whiteness.

The anchoring scape usually grows enough to permit the opening flower to assume an inclined position in the water. Protection from the water is afforded to the exposed floral parts by reason of their waxy texture. The flower comes to rest with a portion of its weight resting on the sepals and the margins of the stigmas. This produces a slight depression about the flower, which is abruptly declined at its inner margin, next to the pistillate flowers. This sloping surface film plays an important part in capturing the floating staminate flowers, and later is intimately connected with the actual transfer of the pollen to the stigmas.

The staminate flowers are borne within the globule spathe which remains on a short stalk at the bottom of the pond. Massed within the spathe, these flowers are joined to the axis by slender pedicels of varying lengths.

The pollen-bearing flowers, very tiny and simple in structure consist of three sepals, two functional stamens, and rudiments of petals. The sepals are of unequal size, two being similiar and nearly opposite, while the third is smaller and placed between them. The two stamens stand close together and have their filaments united up to a point near the anthers.

When the flower is mature, the tip of the spathe opens slightly and the staminate flowers detach themselves from their thin stalks. The uppermost are the first to be shed, taking two or three days to empty a single spathe. The flowers being detached, slowly rise to the surface of the water. The sepals of the staminate flowers completely surround the stamens until after the flower reaches the surface. They then slowly unfurl, the smaller ones opening first, for they seem to orient the flower. This tiny flower with its upraised stamens and pollen mass, keeps its equilibrium by the three broad areas of contact.

The floating staminate flowers are carried along by the wind and coming within the area of the declined film surface of the pistillate flower, slide into the depression, where possibly fifty flowers may be caught. The inner sepals of the captured staminate flowers now in contact with margins of the pistillate flowers. While any further movement of the water,

greater depression of the film results and the pollen is likely to be transferred.

At a certain stage of depression, however, the lateral pressure of the water breaks the surface film and the sides of the cup come together, causing the pistillate flowers to come together in a common bubble beneath the surface of the water. This process has completely overturned the staminate flowers and in this way the latter are inverted upon the pistillate flower resulting in a transfer of pollen. Release of the tension causes the bubble to break, and the flowers resume their original positions. In this process any degree of depression is helpful and complete submergence, although probable, is not necessary to adequate pollination.

The pistillate flower is now withdrawn into the water by the coiling of the scape, where it remains until the seeds are developed. Other examples of this rare type of pollination may be found in several of the Potomogetonaceae and Najadadaceae, which are completely submerged.

Bird Pollination -

A great deal of study has been given to the relation of insects to flowers. Equally interesting and not so well known is the analogous interrelation of flowers and birds. Birds may be classed among the rarer agents of pollination. In Europe, perhaps, no authentic cases of regular pollination by birds are known, but in the Tropics, Central, South, and North America, South Africa, Phillipine Island, New Zealand and Madasgascar, birds play a definite and prominent part in this work. Fritz Mueller, whose researches into the pollination of plants are known to all botanists, says, "Hummingbirds, which constitute one of the most important groups of pollinators, are on wing in Brazil throughout the year. Their activity in visiting flowers is far greater than would appear from accounts known to me. I could almost believe that the list of flowers not visited by them would be considerable smaller than a list of those that are visited."*

At the present time "bird-flowers" are found distributed in the Tropics and sub-Tropics. The birds which visit them include, in the Old World, the pencil-tongued parrots, the tailor birds, the honey birds and the honey eaters; while in the New World it is chiefly the humming birds (Colibris) which visit flowers. The bird-flowers lavishly produce a sugary nectar which the birds drink. This nectar is produced in such large quantities that the natives gather it and use it as part of their food supply.

*Review of Reviews -- May 1925 -- Page 543

Bird-flowers attract the birds by means of brilliant colors, which resemble the plumage of the birds themselves. Perfume does not play an important part in enticing the birds, especially the humming birds, as their olfactory sense is very degenerate.

The tropical abutilus are flowers almost entirely fertilized by the humming bird. Fritz Mueller says again, "A large and beautiful humming bird, the black breast of which shines like a glowing coal whenever the bird is in any way excited, has, with his inconspicuous wife, made himself almost complete master of the Abutilus in my garden. All flowers that are not under cover are pollinated by him."*

A Nicaraguan plant, Marcgravia, has large pendulous flowers which hang in circles, perhaps a dozen from one stalk. As this plant is a climber, the flowers hang aloft in mid-air, below which the numerous nectaries sway, holding considerable quantities of nectar. This nectar attracts many humming birds. As they drink the nectar, their backs rub against the drooping stamens and quantities of pollen is thus transferred to the pistil in later visits to pistillate nectaries.

Though small birds, such as honey-suckers and humming birds, form the large majority of bird pollinators, yet in large flowers, such as the Carolinea, larger birds discharge this duty. In this flower, which is too large for humming birds to pollinate, it is the woodpeckers who, in searching for insects, perform this function.

Of course the bird agents, of varied types and needs, must

* Mueller -- Fertilization of Flowers -- Page 98

be accomodated by the flowers themselves. Thus those which the humming birds visit enable the birds to drink while they are actually on the wing. Bird-flowers are also generally marked by the anatomical structure of the nectar-secreting glands. In some cases the flowers even have solid instead of liquid nectar. A remarkable case of this kind is found in the climbing plant Freycinetia funicularis, which is a native of Amboina. These plants have certain petals which are short, thick, and sweet as sugar, and sealingwax red in color. These are considered delicacies not only by birds but by other animals, such as bats and squirrels, and are found appetizing even by mankind.

What the birds seek in bird-flowers has been definitely answered by investigators. They seek nectar alone. Such insect food as they take they normally obtain outside the flowers. The flowers even possess special devices for excluding insects from their blossoms. The nectar not only satisfies the bird's thirst, but its extraordinary richness in sugar makes it a source of energy for the great muscular labor required in flight.

The bird-flowers are scentless and produce nectar in large quantities. The styles, stigmas, and filaments are strikingly rigid, evidently in relation to the vigor of their visitors. In Strelitzia there is a platform provided. This provision is rarely found in bird-flowers as usually the bird sips the nectar while hovering over the flowers.

Flowers visited by birds are almost invariably red or scarlet. In the tropics, where there are over five hundred species of humming-birds, there are scores of scarlet bird-flowers, as Kerner

has shown, where neither the humming-birds of America nor the sun-birds of Africa nor the honeysuckers of Australia are found, scarlet blossoms are noticeably absent.

Perhaps the reason why the birds have not received the credit that is due them as pollinators is because some of the species are so similiar to certain species of Lepidoptera, known as the humming bird moths. Frequently these moths have been given the credit, while the credit is really due the humming bird.

Insect Pollination -

Introduction -

The symbiotic relation between flowers and insects is regarded as the most wonderful phenomena in the realm of nature.

Zoologists are quite justified when they assert that many of the developments of the bodies of insects are correlated with the forms of particular flowers. But equally true is the assertion of the botanists that many properties of the flowers are likewise in correlation with the shape and habits of flower-seeking insects.

The diversities of color in the animals which visit flowers, the various kinds of mechanism of flight exhibited by beetles, flies, bees, butterflies, and birds, the multiplicity of organs by means of which they extract their food from the flowers, their means of attachment to the blossoms, their fur and bristles for brushing off the pollen, have all their corresponding variations in form and coloring amongst flowers, and consequently there is an equally long and apparently parallel series in the realm of plants.

Inducements offered by the Flowers -

There are various inducements offered by the flowers to the insects and small birds, for example, care of young, desirability of protecting themselves from storms, and most

common, desire for food. Flowers provide these things but receive in return the transportation of pollen to other flowers, an absolute necessity for the formation of a new individual.

Flowers as Nests for the Insects -

Nocturnal Lepidoptera of the genus Dianthoecia lay eggs in the flowers of Caryophyllaceous plants, e.g., the Bladder-campion and Ragged Robin. The female deposits the eggs in the ovary of the flower by means of a long ovipositor. When the caterpillars develop they live on the ovules and young seeds in the placenta. When the caterpillars are mature they bore a hole in the side of the ovary and descend to the ground.

Flowers as Shelters for Insects -

Only beetles, flies and Hymenoptera of the genera Meligethes, Melanostoma, Empis, Andrena, Cilissa, and Halictus use flowers as shelters or for temporary refuge. They are nomadic in their habits, seeking shelter in any quarters where there is sufficient food in addition to a warm retreat.

In the Bell-flowers (Campanula) and the Foxgloves, the interior of the flowers have a higher temperature than the outside air at night. Several Composites, whose outer ligulate flowers close in the evening, are used for shelters by small beetles. When the insects leave the flowers they inevitably brush off some of the pollen which they carry to other flowers in future visits.

Many insects remain in flowers during the day,

sometimes for several days., for example, the beetles of the genera Anthobium, Dasytes, and Meligeeties, which remain in the interiors of the flowers of Magnolias and Gentians. The flowers of the Holly (Papaver somniferum) have within their interiors many flies and beetles which do not leave until the petals drop.

Pollen as Food for the Insects -

Next to honey, pollen is the principle food which animals seek in flowers. In the Poppy and Anemone, the flowers, when open, stand erect, having a cup-like form so that the pollen remains on the concave upper surface of the petals after it is shed from the anthers. These flowers have a special construction because they have no need of a special contrivance for the secretion and storing or protection of the honey.

Bees and humble-bees collect pollen in large quantities and carry it to their nests as food for the larvae. These insects possess specially constructed hairs and bristles over various parts of their body which aid them in collecting the pollen. Some of the hairs are soft and act like a dusting brush. Bees and humblebees have brushes on the terminal segments of their hind-legs which enables them to comb and sweep off the pollen. These insects have special contrivances on their legs similiar to baskets. These baskets are smooth, sharply-defined hollows, hedged in by stiff rod-like bristles, in which the pollen is pressed.

Flowers which contain no honey and offer only pollen as

food, e.g., Poppies and Roses, are characterized by a large number of stamens which provide an enormous amount of pollen. Flowers which conceal honey in their depths are very economical with their pollen. Thus the visitors do not eat the pollen or collect it or carry it to their nests but rather seek the honey in the flowers.

Other Substances used as Food -

There are dusty, flour-like coverings on certain flowers which are similar to pollen in appearance. They are masses of loose, round cells which lie on the upper side of the young petals. These loose cells, which can be seen on the lip of some Orchids, serve as food for insects. These cells are, however, comparatively rare. In the flowers of the Portulaca (*Portalaca oleracea*) there is a cushion covering the ovary. This cushion contains papillae which secrete no juice, but are sucked by many insects and are sometimes eaten. The same is true of the delicate hairs which beset the staminal filaments of the Mullein and Spiderwort. In several species of the genus Lysimachia, the ovary is covered with small warts whose juicy cells are sucked or devoured by animals.

Another substance used for food is found in certain portions of flat petals which consists of a cell-tissue which can be easily perforated and sucked by the mouth-apparatus of insects. Butterflies have, at the end of their maxillary laminae, certain sharp-pointed appendages with which they first tear up the juicy tissue and then steal the liquid.

A special allurement to those insects which are accustomed to juice and suck juicy tissues, is seen in a species of Eremurus. When the anthers dehisce, the petals shrivel and form a small red-brown ball, from which spring six thick greenish swellings. These swellings resemble green aphides. They are really the juicy veins of the under sides of the petals. The fly Syrphus pirastri which seeks aphides for food pierces these swellings mistaking them for the insects.

In Calandrinia, Tradescantia, and Villarsia the flowers when they wither, fall off. Then the cell-sap exudes from the tissue and covers the surface with a thin fluid. Flies suck this juice, while at the same time covering the stigma with pollen.

Honey as an Attraction to Insects -

The secretion of juices on the surfaces of fresh tissues of flowers that remain open several days occurs in 90% of flowers visited by insects and humming-birds. It has a sweet taste and varies in content, consistency, color, and smell.

The secretion of honey takes place in many cases through stomata which are either uniformly distributed over the surface of the tissue, or collected together in particular spots. The amount secreted varies with different plants. In some, the honey forms a thin layer, in others the drops flow together to form larger ones which fill the grooves, depressions and cups prepared for their reception. The sugar which forms the important ingredient of honey is in solution because of its chemical

properties and because it is hidden in grooves and tubes of the flowers and thus less exposed to evaporation.

In some plants the honey flows into receptacles where it is stored, e.g., Coryanthes, Melianthus, Viola, and Linaria. In Coryanthes there is a collecting-cup which receives the honey; in Melianthus there are two narrow petals from which the honey drops into the cup-shaped sepal; while in Linaria the honey is secreted at the base of the ovary where there is a narrow cleft between the two longer stamens through which the honey flows to the hollow spur of the corolla.

There are rare instances in which the formation of honey is carried on by the carpels, e.g., several Primulaceae, and in many Gentians. In the former the slightly arched roof of the ovary secretes minutes drops of nectar, while in the latter, the thickened base of the ovary possesses five cushions which exude honey into the base of the flower.

Nectaries -

Nectaries are frequently found on stamens, e.g., Whortleberry and Bog-whortleberry, where the honey is secreted at the base of the filament. In the flowers of most Papilionaceae the stamens form the nectar. They are fused into a tube, into which is poured the honey from the adjacent part of the staminal tube.

In many flowers the honey is secreted by the floral-leaves, both in flowers where they form a perianth and also in those where they may be divided into calyx and corolla. The

perianth of Tricyrtis pilosa, is composed of six leaves, the three outer ones are expanded near their base and secret nectar. Other examples may be seen in the numerous species of Fritullaria, each of the perianth-leaves having a thickened base which secretes a large drop of honey.

Although honey is seldom secreted by the calyx, examples may be found in the various species of the genus Cuphea and in the Nasturtium (Tropaeolum). In the latter the honey is secreted in the narrowed lower portion of the spur.

Finally, there are nectaries developed at the base of the flower in the region of the corolla. In the Alpine Roses and Monotiopa, the portion of the corolla secreting honey is thickened and fleshy, each of the petals fusing together forming a hollow in the groove at the base. In the corolla of the Valerian the honey is manufactured in a small expansion on the side of the corolla tube; in the flowers of the Pansy, one of the five petals has a honey-spur; while in the Columbine each petal has a spur. In Hypeceum the flowers have two opposite petals which are divided into three lobes. Under the central lobe, a large pit is developed which is filled with the secreted honey.

There are remarkable nectaries which are interpolated between the floral-leaves and stamens, e.g., in Droseraceae, Berberidaceae, and Ranunculaceae. These are commonly called "honey-leaves." All the honey-leaves, although varied in form, may be considered either as modifications of petals or of stamens.

Exposed Nectaries -

Exposed nectaries are accessible but only appropriated by certain insects, e.g., in the spinale tree etc., the honey cannot be sucked up by insects with a long probosces. The thin layer of honey is suited to insects with flatly extended probosces, e.g., innumerable flies and gnats. Insects with short probosces, particularly wasps, seek the large drops of honey in the depths of the lip of the flowers.

Concealed Nectaries -

Concealed nectaries are inacessible to insects with short probosces but are sought by humming-birds, butterflies, and humble-bees. The inaccessibility is modified by the length of the probosces and the depth of the hiding-place. This depth varies from a few millimeters as in the Heath, to sixteen centimeters as shown in those of the Rubiaceous which grows in Sierra Lione. A species of Angraecum sesquipedale, has a hollow spur thirty centimeters long which is filled with honey at its base.

Methods of Concealment -

There are two methods of concealing the nectar. In one, the entrance to the hiding-place is narrowed by all kinds of inflations, cushions, bands, and flaps at the mouth of the flower-tube. The other method is where the nectar is completely closed over by a roof or door, or by two lips. Animals desiring entrance must

either raise the roof, open the door, or press down one of the lips.

In some flowers the stamens form an overarching roof above the honey-secreting base of the flower, as in numerous Salandaceae, Primulaceae, and Campanulaceae. The nectaries may be hidden by the massing together of the stamens, e.g., in the Crowfoots. In these flowers the small nectar-cavity is formed at the base of each petal to which only those insects strong enough to press up the overhanging stamens can gain entrance.

In the flowers of the Phygelious capensis there is a small expansion at the base of the tubular corolla filled with honey which is converted into a closed cavity by the ovary bending down in front of it and pressing itself closer to the wall of the corolla-tube.

Adaptations of Flower to Insect Visits -

The adaptation of flowers with a view to ensuring that insects seeking their honey shall brush off the pollen with some part of their bodies is of so manifold character that it is impossible to deal with all the contrivances. A few of the more striking examples are as follows:

1. Some flowers have prickles or sharp bristles inside. These structures provide routes for the insect's proboscis, thus ensuring the proper one for the deposition of pollen on the back, head or proboscis of the insect.

2. "Revolver-flowers" i.e., flowers which exhibit within their outer portals the open ends of a number of small tubes resembling the barrel of a gun. In flowers of this sort, for example, Bindweeds and Gentians, the anthers are so placed with their pollen-covered faces in

front of the mouths of the tubes, so that insects inserting their proboscis are bound to rub against them.

3. Flowers of the Wild Mustard(Sinapis arvensis)- the anthers after dehiscence, execute spiral twisting which turns the pollen away from the stigma and places it near the slit where the insects insert their proboscis for the honey. This is true in several other Cruciferae, the filaments bend, bringing the anthers into the line of entrance to the nectar.

In the above cases the pollen pours in large quantities from the anthers and forms puffy masses or else a viscid mantle clothing the style. The insects come in direct contact with the pollen, where it is directed in a path where it could not possibly be avoided.

In another method of attaching pollen the pollen is not directly accessible but is hidden in tubes or recesses and the covering must be removed before the insect can be covered with pollen, for example, the corn flower, Centaurea cyanus.

Opening of the Passage to the Interior of the Flower -

The removal of pollen can only take place when the perianth-leaves permit access to the base of the flower.

In the vine(Vitis) the petals fall away on the opening of the flower, however, this is a rare condition. The petals are no attraction for insects but their removal is necessary for easy access to the base of the flower. The petals separate from the flower, curl up, and drop off when the stamens expand.

Access to the interior in the Rampion is obtained by the

development of wide slits between the petals, sometimes there being an entire separation of their free ends from one another.

In some flowers, as in Roses, Anemones, Peonies, the flowers open wide like a saucer. The opening of the petals is sometimes very rapid as in the case of the Evening Primrose, (Oenothera grandiflora), the petals springing apart within thirty seconds.

Many flowers open early in the morning with the rise of the sun, e.g., Wild Roses, Flax and Willowherbs. The duration of flowers varies from three hours to eighty days. These remarkable differences are connected with the amount of pollen produced in the flowers, and with the number of flowers on each plant. They also depend on whether or not the flower is dependent on insects for pollination. Flowers with numerous stamens and ample pollen remain fresh only a few days while flowers with but a single stamen remain fresh often for weeks. The longer the flowers are open the more chance they have of being visited by insects.

Observations point to the fact that the opening of flowers is promoted by the sunshine. This is not easily explained as the observations offer no satisfactory explanation. It is still unsolved in many plants how periodic movements not depending directly upon change in the environment have become hereditary.

Reception of Welcome Insects -

A consideration should be given to the arrangements which enable the insects to obtain the food they desire without loss of time or exertion, and, at the same time giving an advantage to the plant itself.

In many cases the old flowers which do not need the visits of insects bend down out of the way of the younger flowers. In Morina persica, the old flowers not only bend down but also change to an inconspicuous color. In general, the flowers become conspicuous and accessible only at a time when it is advantageous to the plant, opening towards the side from which the visits of the insects are expected.

In flowers such as the Foxglove and Campanula, the flower-stalks bend down and are therefore unsuited to visits of insects which would suck the honey, or those hovering flies which lick up the honey from a flat surface. Bees and bumble-bees cling to the projecting stigmas, style, and stamens and easily climb up to the honey-secreting dome of the bell.

In a number of Papilionaceae the flowers are placed so that the standard is above the keel. In this position the keel is a convenient platform for visiting insects.

In the majority of Orchids the ovary undergoes a spiral twisting which brings the lip below so as to serve as a platform for the insects. In Vicia, Corydalis, and Penstemon, the flowering axes turn towards the same side, so as a one-sided spike results. In the Horse Chestnut and many Liliaceae the stamens or style which project well beyond the margin of the flower also serve as a landing place.

The various arrangements which aid the insects in their visits to flowers are as follows:

1. The margin of perianth or corolla is modified, e.g., Aristolochias.

2. In Aristolochia labiosa there is a broad heart-shaped expansion in front of the narrow entrance to the flower.

3. In Aristolochia cordata there is an elongated perch for flies.

4. In Aristolochia clematitis there is a slightly excavated lip on which the midges can alight.

5. In Phalaenopsis schilleriana there is a smooth and complex labellum which has a small projection which serves as a footstool to visiting flies.

6. In Ophry cornuta there is a lip which has two hollow projecting pegs.

7. In the Snapdragon there are two knobs which project from the lower lip, serving as a platform.

8. Many Papilionaceous flowers which have five petals, the two in front forming the keel, the two lateral ones forming the wings, and the posterior one forming the standard. The standard closes the entrance to the base of the flower, where the honey is concealed, so that the insects must alight on the keel or wings.

Accessory Floral Features.-

The whole of that complicated structure which we commonly designate as the "flower" of a plant consists, in point of fact, of the reproductive organs, enclosed in a number of envelopes which have for their purpose not only the protection of the essential organs within, but also the attraction of those insects and other

animals which are necessary for the fertilization of the ovules. The contrivances for effecting this purpose, though infinite in number and variety, may be classed under two principal heads, color and scent. Where the juice of the flower does not seem to be scented, the bright color of the corolla commonly serves the purpose of attracting the animals. Hummingbirds, as said by Delphino, have a penchant for scarlet flowers with long tubes, while others, such as the carrion flower and skunk cabbage, attract the flesh fly by giving off an odor resembling decayed flesh.

Color -

A study made by Dr. Frederick Clements and Dr. Frances Long of the staff of the Carnegie Institution, gives an understanding of the attraction of flowers. It was shown by their experiments that blue was the most popular color, while red was the least. They concluded that the main attraction of flowers for pollinators was both by color and odor and that the pollinating agents are also guided in their movements by form and markings, such as stripes and dots. A striking fragrance will attract at a distance, while color exerts its influence only within a radius of thirty feet. Form operates chiefly within a few feet, and the guide-lines only serve as a last resort.

Sometimes the stamens act as attractors. Willows, lacking perianth-leaves, are conspicuous because of closely crowded stamens with red or yellow anthers. In certain Ranunculaceae, e.g., Actaea, the

stamen-filaments are brightly colored. The North American Pachysandra stands out from the background because of its white dazzling filaments. In several Asiatic steppe-plants, there is a bladder-like appendage which rises above each anther, which is brightly coloured, yellow, violet, or dark red.

In many flowers the bracts are brightly colored and are in contrast to the surroundings. Many examples may be found, e.g., in Genetyelis tulipifera, Nepeta reticulata, and Carlina acaulis.

Another method of rendering the flowers conspicuous is by the massing together of flowers into bunches, spikes, racemes, umbels, or capitula. The flowers are so small that if single they would hardly be seen at a distance.

When the bracts have the function of attracting the insects, they are usually aggregated. The effect of colored envelopes is materially increased when the flower heads are massed together forming dense tufts.

Much has been written about the protective coloring among birds and animals, which melts their plumage or furs into their surroundings and cloaks them with a mantle of invisibility. But coloration among the flowers is just the reverse of protective. It is a trumpet-call to attract attention to them. Just how much of a rôle color plays in attraction we do not know, but Darwin, Mueller, and Lubbock believe it to be of highest importance.

In the Lavender the bracts have become a peculiar source of allurement. There are some which grow on the lower half of the spike which are insignificant, while those growing at the top of

the flowers are enlarged brilliantly into tufts which makes the flowers very conspicuous.

Often the flower possesses several colours. In the Herb Paris, Paris quadrifolia, the bright yellow anthers encircle the large, dark violet ovaries. In the center of the flowers of the Borage, Borago officinalis, a black cone of anthers rises from a blue star, and a yellow cone of anthers on a violet star in the Bitter-sweet, Solanum dulamara.

In hundreds of flowers the petals are made conspicuous by spots, speckles, stripes, bands and borders. There is a brilliant contrast caused by the difference in the colours of the corolla and the outspread bracts and sepals, e.g., in the flowers of Acanthers, the upper sepal is violet while the petals below are white. In Composites the florets of the rays and of the discs are usually differently coloured.

Contrast of colour is sometimes produced by the corollas changing their colour at various stages of development. In the bud they are red, after opening they become violet, and when they whither they become blue or green, e.g., in the Bitter Vetches, and several Boragincous plants. In the Telekia, Telekia speciosa, the flowers of the head are yellow at first, but later become brown, In some of the Cruciferae, the green sepals change to a yellowish colour.

Zoologists believe that animals that visit flowers possess a highly-devloped colour sense. White is a colour which is not only best seen in the dark, but can be plainly distinquished in

bright daylight. Dark brown is very attractive to wasps, perhaps because it resembles decaying flesh.

It is probable that in many floral regions the predominance of certain floral colours at various seasons is connected with the distribution of animals at that time.

Such facts prove that the colouring of the flowers is related to insect visits. Von Hess (1913) experimented and made a comparison between colour sight in insects and colour-blind human beings. He found that the graph for bees and other invertebrates, measured by using phototropic resonse, corresponded with that of totally colour-blind men. He concluded that these animals were colour-blind and could only perceive differences in light intensity. Von Frisch stated that Von Hess had not deducted correctly from his experimenting and carried out experiments which seem to give conclusive evidence in favor of a limited colour sense. He found that the bee can distinquish yellow and blue, but not red or green.

The bee, therefore, can see yellows, blues, and purples, and the colour of the flower affects its senses. Thus we have an experimental explanation of the facts that bee flowers are generally blue or purple in colour, and that yellow is frequent.

Sprengel, and other biologists have described the various markings on the general ground colour of the corolla as "honey guides." A familiar example is the dark lines running towards the base of the petals in the violets.

Von Frisch experimented and concluded that the form sense, including the power of distinquishing between colour patterns, is important in enabling the bee to pick up the particular flower it is

visiting from other similiar flowers. It is probable that they make identification of the flower to be visited easy, and that this is its chief function.

Scent -

The possession of a keen olfactory sense by pollinating insects is undoubted yet difficult to detect. There is a great difference between the sense of man and other animals according to the different degrees of sensitiveness of their olfactory fibres. There may be nerves in the olfactory organ of some animals sensitive to the particular form of molecules which appears scentless to man. This explains the fact that flowers are eagerly visited by some insects but ignored by others.

One of the most remarkable correlations between flower scent and insects is the development of the scent simultaneously with the time of flying.

The close correlation between insects and the odor of flowers may be shown in certain species of Honeysuckle which smell very faintly during the day but after sunset give off an abundant odor when the ocrepuscular Lepidoptera are flying about. On the other hand, many flowers visited during the day are scentless at night, for example, in the yellow flowers of Spartium scoparium. The same is true of the Grass of Parnassus which only gives off an odor of honey in the sunshine and becomes scentless in the evening.

Colour and scent in flowers to some extent mutually exclude one another, so that in cases where the allurement is brought about by colour, the scent is absent and vice versa. However this is

not always so, as shown in many tropical Orchids, Magnolias, Roses, and Pinks, that have both bright colors and strong odors.

A uniform distribution of odorous substance over the plant is rare; much oftener the scent of the flowers differs from that of the foliage, e.g., in the Garlics which have a scent of honey in their flowers while their leaves have a strong odor which serves to protect them from grazing animals.

Scents may be combined in a flower, thus making them hard to detect, However, there have been about fifty seents distinquished which are classified into five groups, (1) the indoloids, which arise from the decomposition of albuminous compounds, (2) the aminoids, which have an amine as a foundation, (3) the bengaloid scents which are compounds of a benzole nucleus, (4) the paraffinoids which produce valerianic acid, and (5) the terpenoids which are produced from etheral oils destitute of oxygen.

It is very noticeable that similar plants often have different scents, e.g., in Gymnadenia conopsea, the odor of cloves, while in Gymnadenia odoratissima, the odor is vanilla.

The general conclusion is that colour is the guide to the flower, and that scent is useful in enabling the bee flying among many flowers of similiar colours to pick out the species it has formed the habit of visiting. This conclusion cannot be applied to insects in general.

Pollinating Insects -

Bees -

Bombus and Apis are the most efficient of all pollinating insects, mainly due to their extensive activity, their precision, and their adaptation, such as hairy legs and long proboscis for obtaining nectar from tubular flowers. To the flowers, the bees became important visitors and it is to these important pollinators we now turn in our study of insect pollination.

The highest types of cross-fertilization occurs in the Orchids. Their flowers, through long ages of adaptation, having gradually shaped themselves to the forms of certain chosen insects: bees, butterflies, and moths. The pollen in the Orchids is seldom dry and powdery, but is usually waxy and often made up into a club-shaped mass, or globules bound together with minute threads.

We find three distinct methods of effecting cross-fertilization in the Orchids. In the first, as in the Lady's Slipper or Cypripedium, the insect enters by one opening, passes under the stigma, and departs by another. In the second, as in the fringed Orchids, or Habenaria, the pollen masses fasten themselves upon the head or the tongue of the insect visitor. In the third, as in the pogonias, the pollen is formed and held in a box, which opens and dusts the insect as it withdraws from the flower.

For another example of the work of the bee let us turn to the pink Lady's Slipper. The gay, pink pouch of the Lady's Slipper serves the bee as a landing-stage, and then as its trap or prison.

This pouch is so constructed that the thin slit-like opening will allow the bee to enter, but will prevent an easy escape. The only exit is a passageway which is partly barred. A first obstruction is the column, which is bent so as to place the stigmatic surface in the narrow opening, and then, higher up, there are two pollen masses. Thus the bee must touch the stigma and also receive some pollen on his back when he departs from the flower.

Another example of the adaptation to cross-fertilization is in the Orchis spectabilis, or showy orchid. The flower consists of a purple hood or cowl, overhanging a white bib or lip, and shelters an erect, white column. At the foot of this column there is a small opening which gives access to the concealed nectar. Just above the nectar, the adhesive stigmatic surface is found, while above this there are two curving pollen-pockets. When the bee arrives on the white lip, it thrusts it's tongue down the well in search of the nectar. While doing this it rams it's head against the pollen which is in the form of discs. At first the pollen discs are erect on the head of the bee but soon they droop forward so that when the bee visits the next flower, they will be in the exact place to touch the stigma.

Entrance to the orchid is complicated by various devices; by the position of the lip upon which the insect must alight, the narrowed opening of the throat of the flower in front of the nectary, and a fissure in the center of the lip. In the flowers of the milkweed the pollen is in the form of pollinia connected in pairs, having a special organ of attachment. This attachment is aided by the connecting knob which is hard and dry with two arms capable of holding an object,

the pollinia are in the form of shiny horny leaflets and (3) they belong to two adjacent stamens not to one. As all parts of the flower are smooth and slippery, the only way the insect can support its weight is by inserting its claws in the slits between the anthers. When the feet are withdrawn the two pollinia adherent to the clip are dragged out of their niches. When the foot is later placed into a stigmatic chamber the ligatures are broken and the pollinia are left in the chamber, while the actual clip maintains its grip of the claw. This clamping of pollinia to the feet of insects is quite unique amongst phenomena of the kind observed in the whole realm of plants.

When we observe the actions of bees as they visit the flowers, we frequently notice very curious arrangements of the corollas, such that the bee, in seeking the nectar in such flowers is sure to have some of the pollen fastened on its body in a position where the dust will be brushed upon the pistil of the next flower which is visited. Drs. Clements and Long have found that bees have excellent memories. They found that they not only remember places, but also colours, odors, and shapes. For example, "When the nectar flow of the buckwheat takes place during the day, it is an illuminating experience to watch a bumble bee fly to a lotus plant, visit everyone of the orange blossoms and touch none of the yellow blossoms, in which the nectar flow has ceased as they fade to this color."*It is evident that flowers have become beautiful by their struggle during the ages, since the coal period to attract the insects, and that these creatures, especially the bees, have bodies, modes of life, and instincts adapted to

*Clements and Long -- Handbook of Flower Pollination --Page 43

relations to flowers. Nowhere else in the realm of life can we so at a glance perceive how profound is the interaction between all living beings, however diverse they may be, when the needs of life bring them in contact, as in these exchanges of insects and plants.

Moths -

The beautiful night-blooming evening primrose presents an interesting adaptation to moths. The tube is long and slender, and the nectar secreted at the farthest end. Only a tongue an inch or so in length could reach it. What insects have tongues of this length? The answer lies with moths and butterflies. The primrose blossoms at night, when the butterflies are inactive, and is thus clearly adapted to moths. The projecting stamens scatter the loose pollen upon the moth as it seeks the nectar. As this flower is only pollinated by moths, we find it only opening at night and remaining closed during the day.

One of the most common of American Orchids is the little Habenaria orbiculata found in damp woody places. The flower has a structure so remarkable that without close study no one could imagine the use of the varied parts. After examining the flower we find that the strap-shaped puce in front is a petal, the opening at the top leads into an elongated nectar tube and that the two structures converging above this opening are the halves of one anther, each of which contains pollen masses, fastened together into a sticky disc. The darker space between the anthers and the opening is the stigma. The insect which pollinates this flower is a moth with a long proboscis that can reach

to the base of the nectary. As it reaches for the nectar, the insect's eyes come in contact with the two sticky discs, which immediately attach themselves to the moth. In this way the pollen is carried off and reaches the pistil of another flower when the moth pays a visit to a pistillate flower.

The most wonderful device by which plants are pollinated by moths may be found in the genus Yucca which is pollinated by *Pronuba yuccasella*.

The flowers are bell-shaped and are arranged in large panicles which are suspended at the end of a smooth, green stalk. The six perianth-leaves are yellowish-white and can be seen at night from a considerable distance. When the petals open the small anthers which are placed on thick, velvety filaments, dehisce exposing the yellow adhesive pollen. At night, the female of the genus *Pronuba yuccasella* penetrates into the interior of the flower in the search for pollen. The first joint of the maxillary palp is lengthened, in the female, and has its inner surface covered with stiff bristles. This appendage, which can be rolled up, is used to collect the pollen and form it into a ball which is placed under the head. When the large ball of pollen is collected, the moth flies to another flower and after finding a favorable spot on the surface of the pistil, she lays her eggs. When this process is completed, the moth flies to the top of the stigma where she unrolls the trunk-like palpi, stuffing the ball of pollen into the stigmatic funnel. When the larvae develop, they bite a hole in the succulent wall of the ovary, finding their way to the ground.

If it were not for the transfer of the pollen by *Pronuba Yuccasella* the ovaries and ovules of the Yucca would not ripen into seeds.

It has been ascertained beyond a doubt that the larva of the moth lives exclusively on the young seeds of the species of Yucca.

These three illustrations show in a general way, the adaptations of flowers to moths for pollination.

Butterflies -

Butterflies also serve as pollinators and transfer the pollen of many plants. The butterflies feed on nectar and consequently possess special mouth parts, known as maxillary laminae,which are elongated. Like the bees, they are diurnal insects and are able to get nectar which is hidden deep in the flower. This is also true of a few moths.Some of the plants that the butterflies visit include: field larkspur, violets, starry campion, red clover, and button-bush.

Flies -

Another interesting group of pollinators are the small flies, Diptera. For example, in the small herbaceous plant Aristolochia chematitis, yellow blossoms attract the pollen-laden flies. They easily slip down the tube into the nectar chamber by the help of numerous hairs. While working around the nectar in the chamber, they leave their pollen on the stigmas, which soon curl back out of the way of further pollination. When the pollen has reached the stigma the nectar secretion ceases and the hairs wither up, allowing the insect to escape. Finally the flower partially closes at the mouth and droops on its stalk. It is sought no more by insects, as their visits would obviously be useless.

There are many cases in which the insects are held captive after they have entered the floral cavity. The most unique example of this type of insect pollination is found in many Arvideae, e.g., in the Arum conocephaloides. The spathe widens near the top while the lower part expands into a barrel-shaped receptacle. Flies attracted by the foul odor of putrefaction which is given off by the plant, climb down the flower into the cavity formed by the spathe. This cavity is made up of stiff bristles which are curved downward, thus allowing the insects to climb downward but preventing their escape. When the pollen is liberated, it covers the region which bears the male flowers. At this time the bristles become limp and the construction at the top of the spathe is loosened and expanded. As a result of this arrangement the insects become covered with pollen as they make their escape from the flower.

In the Arum conocephaloides there are two layers of bristles. On the lowest part of the spadix are the female flowers, above them the first ring of bristles, next the male flowers, and then a second ring of bristles. The upper layers relax later than the lower ones. The insects are kept in the upper story by the upper bristles until their pollen is scattered onto the female flowers. When this has been done the upper layer of bristles relaxes and the insect escapes.

The drone flies, Syrphidae, have elongated probosces and depend a great deal upon flowers for food. The Euonymus is a typical example of a flower pollinated by flies for it has an exposed nectary and exposed pollen. "Color seems to have but little significance, but odors attract numerous flies; particularly carrion flies

and dung flies, which may thus be important pollinating agents of ill-smelling flowers like Rafflesia."*

Wasps -

There is another remarkable relation between plants and insects illustrated by the fig trees and certain small wasps of the family Chalcididae.

A small wasp of the species Blastophaga grossorum passes into the inflorescence of the fig, depositing there an egg, close to the nucellus of the ovule. The white larva which develops from the egg fills the entire cavity. The ovary has now become a gall. The wingless males are the first to emerge, having fertilized the females before biting their way through the gall wall. When the females leave, they pass through the mouth of the flower thus coming in contact with the pollen. After emerging they lay their eggs in flowers in an early stage of development, thus powdering the stigmas in the process. No seeds are formed in the gall-flowers, owing to the fact that the eggs of the wasp are laid in their place. In those species of fig in which gall-flowers are not especially provided, the eggs are laid in a certain portion of a normal female flower, not converted into a gall for the style is too long for the ovipositor of the female so that the egg cannot be inserted quite into the ovary, but is left in a spot favorable to development. The gall-flowers are adapted to the reception of the egg at the spot where the ovule would otherwise devel-ope as they are not adapted to the production of seeds capable of germination, as no pollen-tube can develop upon their abortive stigmas.

*Coulter, Barnes, and Cowles -- Textbook of Botany -- Page 842

"The wasps which deposit their eggs in the figs carry the pollen both to the short-styled gall- flowers and to the long-styled ordinary female flowers, and attempt to lay their eggs in both kinds of flowers. "*

In southern Europe where the figs are extensively cultivated, the majority of trees planted are Ficus, i. e., having only female flowers. Caprificus, besides male flowers, contains only gall-flowers, and is not cultivated.

An accurate and vivid description of this unique correlation between the production of figs and the wasps which pollinate them may be found in the following words of Skene: "The wasps pass the winter in the mamme of the caprifig, and, escaping about March, enter the profichi of the caprifig and also the "fiori di fico" of the fig. In the former they lay their eggs in the gall flowers; the latter contain sterile female flowers only in which eggs cannot be laid. The fiori di fico ripen in some varieties, and are edible, but usually they fall off. From the profichi the gravid females escape in June, becoming dusted with pollen as they make their way out. They then enter the "mammoni" of the fig and the "pedagnuoli" of the caprifig. In the former they find gall flowers in which they lay eggs, in the latter they pollinate the female flowers which alone are present. The pedagnuoli ripen into edible figs from August to December, and form the main crop of all varieties. From the mammoni a new generation of gravid female wasps escapes in September, and these sparingly dusted with pollen from a few male flowers, pass to the mamme of the caprifig, in the gall flowers of which the larvae pass the winter. They also enter the "cimaruoli" of the fig, in which only female flowers are present."*

* Skene -- The Biology of Flowering Plants -- Page 82

Classification of Entomorphilous Flowers -

Mueller divided entomorphilous flowers into nine classes:-

A- Pollen flowers are without nectar, but with a super-abundant production of pollen which is gathered for food, especially by bees. In some flowers special "food pollen" which has lost, partially or completely, the power of germination, is formed in special stamens, as in Cassia.

B- Flowers with exposed nectar, such as the Umbelliferae, Maples, and the Elder. The flowers are small, wide open, and with abundant nectar. They are visited by short-tongued flies, ichneumons, and beetles.

C- Flowers with partly concealed nectar, such as the Buttercups and many cruciferae. Dipterous flies and short-tongued bees can easily reach the nectar although it is partly hidden by hairs and scales in short corolla tubes.

D- Flowers with fully concealed nectaries in which the nectar lies at the bottom of a long tube and may be only obtained by insects with long tongues, e.g., bees, butterflies, and moths. Examples of this type of nectar may be found in Heaths, Forget-me-nots, Mint, and Thyme.

E- Inflorescence with concealed nectar. The inflorescence resembles a flower and acts as a single flower in attraction. Compositae illustrated this class.

F- Hymenopterous flowers are almost exclusively visited by bees. In some the nectar is very deeply placed so that only an insect with a long tongue can reach it, as in the Red Clover. In the Snapdragon

and others, only a heavy insect can open it. In some zygomorphic flowers, like the violets, orchids, and sage, a convenient landing stage for the bee is combined with deeply concealed nectar at the base of a long corolla tube, or in special spurs.

G. Lepidoptera flowers have the nectar concealed in tubes or spurs. Those flowers pollinated by night moths, such as the Honeysuckle and Nottingham Catchfly belong to this class. These flowers are characterized by their stronger odor in the evening and by pale tints easily visible in the twilight. The Madagascar Orchid, Angroecum sesquipedale, has a spur nearly a foot long in which the nectar is produced. Wallace in his essays on natural selection predicted that a sphingid moth with a tongue of the same length would be found. Mueller in 1873 described such a moth in Brazil.

H. Diptera flowers are chiefly visited by flies. In the Cuckoopint, Arum maculatum, flies are attracted by the lurid red color and putrid odor of the terminal portion of the spadix axis. When they crawl into the flower they are held among the female flowers at the base of the flower by a ring of hair-like stamens. They can only escape when these have withered, thus passing by the male anthers which are dehiscing.

I. Small insect flowers which are pollinated by small flies, bees, and beetles. *

* "Skene -- The Biology of the Flowering Plants -- Page 350

Mechanical Mechanisms -

Piston apparatus -

There are various kinds of apparatus for loading insects with pollen. Among these is a pump apparatus in the Papilionaceae which is unique. The two lateral petals called alae or wings converge towards their upper margins so that they form a convex saddle arching over the keel. This may be noticed in the Bird's-foot Trefoil, Lotus corniculatus. The wings and keel are locked together by a projecting fold near the base of the wing which fits into a socket in the keel. When a bee lands on the ridge formed by the wings, the keel is also pressed down. With this movement comes an extrusion of a mass of pollen through a single opening at the conical apex of the keel, which results in the attachment of the pollen to the insect. This process of expulsion is explained by the fact that when the keel is depressed, the stamens, being fixed, are forced further into the conical cavity and thus push a part of the pollen stored in it through the small orifice in the top. This type of apparatus is confined to the Papilionaceae.

Percussive mechanism -

The percussive method of scattering pollen may be found in many flowers. It is called this because the filament striking the insect resembles a hammer striking on a bell.

In Salvia glutinosa, the under-lip of the flower serves as a landing stage. The bee must go into the flower to

reach the honey which is hidden in the back of the flower. The stamens are situated on either side of the entrance which consists of a short, erect, and immovable filament and an anther borne on a slightly curved, elongated connective. The stamen in turn consists of two arms of unequal length in a curved lever. The upper arm is longer and ends in an anther, while the under one is short and thick. When the bee touches the lower arm, the upper arm drops and thus covers the back of the insect with pollen.

In the Lopezias indigenous, the lower part of the insect is covered with pollen. These plants have only a single anther-bearing stamen in each flower. The stamen is wedged in a sterile staminode, which has its free edge fashioned into the shape of a spoon. This affords a landing stage. When an insect alights the staminode suddenly flies down, while the stamen concealed within it springs up, covering the under surface of the insects body with pollen.

Another example of this type of mechanism may be found in the Barberry. In these flowers there are six stamens arranged in two whorls, sloping obliquely outward and concealed by concave petals. The bases of the flowers are sure to be touched when the insect, in order to secure the honey, fastens itself to the pendent racemes. This touch acts as a stimulus and results in an alteration in the tension of the tissues, and also in a sudden-backward movement or up-springing of the stamen. Thus the anther strikes the insect covering its head with pollen.

reach the honey which is hidden in the back of the flower. The stamens are situated on either side of the entrance which consists of a short, broad, and immovable filament and an anther borne on a slightly curved, elongated connective. The stamen in turn consists of two arms of unequal length in a curved lever. The upper one is longer and ends in an anther, while the under one is short and thick. When the bee tries to raise the lower arm, the upper arm drops and thus covers the back of the insect with pollen.

In the Lopezia [illegible], the lower part of the insect is covered with pollen. These plants have only a single anther-bearing stamen in each flower. The stamen is lodged in a bottle staminode, which has its free end fashioned into the shape of a spoon. This affords a landing place. When an insect alights the staminode suddenly flies down, while the stamen concealed within it springs up, covering the under surface of the insect's body with pollen.

Another example of this type of mechanism may be found in the barberry. In these flowers there are six stamens arranged in two whorls, bending obliquely outward and concealed by concave petals. The bases of the flowers are made to be touched when the insect, in order to secure the honey, fastens itself on the nectary organs. This touch acts as a stimulus and results in an elevation of the bases of the stamens, and also in a sudden backward movement or up-springing of the stamen. Thus the anther strikes the insect covering its head with pollen.

Explosive flowers -

Explosion is due to a sudden up-springing of some organ, which maybe the style, the filaments, or, as in a few Orchids, the anthers and rostellum.

In Crucianella stylosa the long, slender style is twisted into a spiral, the thick stigma being wedged between the anthers. When the anthers open, the stigma becomes coated with pollen. With the elongation of the style, the stigma rests against the dome-shaped top of the closed corolla. The instant the corolla opens, the style springs up, scattering a cloud of pollen.

A landing stage is provided in Schizanthus pinnatus by the two lobes which form a keel. In the furrow of this keel are two stamens which are released when an insect alights.

Another example of this type of mechanism may be found in Spartium scoparium. In this flower there is a large, upturned standard having two lateral petals, beneath which is the keel. The pair of petals locks with the keel by a swelling and a depression near the base of each keel-petal. Concealed in the keel is the style and the ten stamens, all in a state of tension. As the anthers liberate their pollen early, it accumulates in the front part of the keel. With the touch of an insect which is seeking the honey, the wings and keel fall with a jerk, while the stamens and style spring up, throwing a mass of pollen into the air.

The Brazilian shrub, Posoqueria fragrans, is adapted to the visits of Sphingidae. The ábundant honey at the base of the flower can be reached by the tongues of only Sphingidae, whose

proboscis are 15 mm. long. The five anthers are united into an oval knob directed obliquely downwards and containing the pollen which has escaped from the anthers before the expansion of the flower. When the insect touches one of the upper stamens which are very tense, they spring up and hurl the pollen against the insect's proboscis.

The sprinkling apparatus -

The pollen is always of powdery consistency and is shaken out of the loculi where it is produced. There are three modifications of this apparatus: (1) the sugar-tongs modification: (2) the anthers dehisce by terminal pores: and (3) the anthers are united in cones.

In the first modification, the filaments are like a pair of surgar-tongs, and the anthers, when in a dehiscent condition, are in the form of spoon-shaped recesses, with their concave sides facing one another. The pollen is kept in these recesses until the separation of the valves, which is caused by insects when they press into the jaws of the flowers in search of honey. The proboscis is either pushed right between the valves, or it strikes against the certain special processes of the valves, or else the tense filaments are forced aside.

As for the second modification examples may be found in the bell-shaped blossoms where the anthers act like pepper-castors. At the extremity of the anthers are two little pores with their holes facing downward. The pollen is tightly compressed in the

anthers, but is sifted out intermittently when an insect visits the flowers, thus setting the anthers into motion.

In many cases the anthers have special appendages against which the insects are sure to strike on entering the flower. The Snow-drops (Galanthus) have simple, rigid points which stand in the way of visiting insects. The Strawberry-tree (Arbutus) has two little horns projecting from the back of each anther, against which insects knock in their quest for honey.

The third type of sprinkling apparatus consists of a whorl of stiff stamens grouped together so as to form a hollow cone. The anther consists of two lobes which open by longitudinal fissures. The pollen is concealed in eight or ten long loculi which part and let their contents fall if the cone is displaced to the slightest degree. When an insect touches the cone upon inserting its proboscis, a shower of pollen descends upon it. The anthers are replaced by means of their elastic filaments when the insects leave the flower. In the Violet and Pansy the cone of anthers is set over the lowest petal, which is prolonged into a spur containing honey. The insect encounters the thickened extremity of the hooked style when it pushes under the cone along the channel of the spurred petal in the quest for honey. When the style is displaced, the closely adhering stamens are affected, and the pollen is scattered on the insect.

PROTECTION AGAINST UNWELCOME GUESTS

Wingless marauders -

There is indirect protection afforded to the floral honey by having it secreted in the region of the foliage. An example may be found in the Himalayan species, Impatiens tricornis. The stipules are modified into secretory glands. They are found at the right and left sides of the bases of the leaves. One gland is small and rudimentary, while the other is well developed, being made up of a fleshy convex disc fused partly to the base of the leaf and partly to the stem. The honey forms in drops on the cushion of the disc. The ants lick up this honey at these stipular nectaries and do not seek the honey further upwards. Ants would only pilfer the honey without touching the pollen or stigma.

Isolation by Water -

There are other ways in which protection is afforded. In unnumerable aquatic and bog plants, e.g., in Water Lilies, Arrowheads, and Bladderworts, protection is afforded by the water against marauders such as snails, centipedes, etc.

Sticky Secretions -

Many plants are protected by sticky secretions, such as, bird-lime, cherry-gum, mixtures of resin, or occasionally by latex. In certain Asclepiads the involucral scales which inclose the flower head abound in latex. As soon as ants reach these scales and touch

the turgid cell layers, the cells rupture and the milky secretion runs out in droplets, in which the ants become involved.

Protection by Glands -

Other adhesive substances arise from circumscribed cells of the epidermis of the stem or else as definite projecting structures known as glands, glandular hairs, capitate hairs, etc.

The secretion in the flat epidermal cells collects between the inner and outer layers of the external wall under the cuticle. The cuticle expands until it bursts, allowing the substance to escape. In the glandular secretion, the substance may pass directly to the surface by diffusion through the walls or by an actual rupture of the delicate walls of the glandular cells. Usually the sticky substance occurs on the flower-stalks or on the main axis of the inflorescence.

More frequent than a sticky coat is the presence of glands or glandular hairs on the flower-stalk or on the outside of the flower itself.

Protection by Wax Coatings -

In many plants the whole foliage is sticky, while in others there is a wax coating on the flowering axis and pedicels which guards against the approach of small creeping insects, e.g., in the catkin-bearing twigs of the Salix daphnoides, ants attempting to climb up the catkins, slip on the wax-covered twigs and tumble to the ground.

Winged Marauders -

Protection by Floral Structures -

Snails, slugs, and such animals are not hindered by sticky secretions but to spines, prickles, and stiff bristles they are very sensitive. Thus these structures placed in the neighborhood of the flowers form a protection against these animals. They do not take just pollen and honey but also devour the petals, stamens, and carpels. There are two features to this method of protection: (1) the number of these structures increases markedly in the region of the flower and (2) these spines, etc. often serve as "pathfinders" to direct the welcome honey-sucking insects. This latter feature applies to the sheathing bract-like investments of many flowers.

Protection by Hairs-

Those structures directed against undesirable winged-insects are situated chiefly within the flower and take the form of hairs and fringes. These may be arranged either in irregular tufts and wholly plugs or into lattice-work, cages, or crowns of hairs. In Atropa, Lycium, and Polemonium, the corolla is smooth inside while the bases of the stamens are provided with hair to screen the nectaries.

Protection by Movement of the Flower -

Protection may be afforded by the bending, twisting, or convergence of various parts of the flower so that honey is hidden in grooves and special cavities.

This protection may be found in (1) flowers with long, narrow tubes, (2) in flowers with various projections, cushions and lobes of the corolla which narrow or subdivide the aperture, (3) and in closed flowers with crowded stamens.

Protection afforded by Periodic Display -

Periodic attraction may afford some protection In the moth-visited Caryophyllaceae, the flowers are purple underneath and white above. In the daytime the lobes are furled so as to be unnoticed by day-flying insects. At night the flower is very conspicuous and gives off a perfume attractive to moths.

Rarer Pollinators -

Although bees, butterflies, birds and moths are the commoner agents of pollination, a consideration of the rarer agents reveals several interesting interrelations. For instance, the fact that certain plants rely upon the bats for pollination has only been discovered within the last few years. In Trinidad, at the Royal Botanic Garden, the work of bats in this respect has come under direct observation. A tree known as the Bauhima megalandra, which grows to a height of about thirty feet, produces each year around January, long, white flowers which blossom in the dusk. When they are in full bloom, the bats come out of their hiding places and fly swiftly from one flower to another. The large, white flowers quickly attract them and they pounce on the blossoms, often to the great injury to the beauty of the flower, for the bat secures itself by seizing the white petals as it settles on the flower. One would naturally imagine that the bats found nectar in these flowers but a close examination shows that the flowers contain no honey, but doubtless harbor many small insects. It is these insects which attract the bats, for they find a generous meal in the depths of the flowers.

A Wallaba tree, Eperua flacata, growing in the same vincity, was also visited by bats. These bats were about the size of a hawk moth and possessed a brush-like tongue, similiar to that of a moth. In the case of both of these trees, there can be little doubt that the transfer of pollen is accomplished by the bats.

Still another plant, a Java creeper, was found to be pollinated by bats. A particular species, the Kalaya, affects this creeper, and it has been seen to tear out the three inner petal structures and devour the succulent tissue. As it eats the flower, it's head becomes covered with pollen from the stamens and while it chews some of the female flowers, the pollen reaches the stigma, thus assuring cross-fertilization. As far as is known, bats play no rôle as pollinators in Europe.

It has been reported that a mosquito has been examined and found to have had two small masses of pollen on its head. After closer study it was concluded that mosquitoes pollinated the Orchid Habenaria obtusata which was abundant in the region where the mosquito was found. This was a startling revelation but later experiments proved this to be true.

Another unique method by which pollen is dispersed is by the agency of Kangaroos. In the low shrub-Australian "Scub" the flowers are arranged around the margin of a cup. At the bottom of the cup, which is lined with scales, drops of liquid collect which is secreted by the flowers.. This liquid smells like sour milk. The styles project around the margin, slightly bent inward. The pollen is collected at the tops of the styles at the beginning of the flowering period. Kangaroos stick their snouts into the inflorescences to drink the sap and consequently dust their mouths with pollen which is conveyed to the developed stigmas. The respective heights of the Dryandia bushes and of Kangaroos and the configuation of the inflorescences compared with the snout of this animal, leads to an assumption that this is a fact.

Among the most curious and the rarest pollinators are the slugs and snails. The plants that are pollinated by them have very small flowers set closely together, as in the Compositae. The Italian botanist Delphino was the first to call attention to this interesting fact. For example, the ox-eyed daisy is frequently visited by a small snail in wet weather when the flying insects are not available. The snail feeds upon the petals and as it crawls around, it carries the pollen from one flower to another. As Ludwig observes, "plants which lack the customary agents of pollination when continuous rains occur during the flowering season and would otherwise produce no fruit, may find in slugs and snails effective substitutes for insects which are only active in dry weather."*

* "Unusual Agents of Pollination" Sci. Am. S. Vol. 64 Page 302

PERFORATION OF THE COROLLA

In many parts of Europe in the United States, and in the Himalaya, bees have been found to bite holes in flowers in order to obtain the nectar. Plants depending on the visits of insects for pollination cannot produce seed if the nectar is stolen from the outside. Darwin found that after gathering hundreds of twigs of Erica tetralix everyone of them had been perforated.

In general, it is humblebees which first bite the holes. They are well adapted to this work as they possess powerful mandibles. Dr. Mueller found that hive bees use the holes made by the humblebees, generally, but also reported that the former had been seen to bite holes through the flowers of Erica tetralix. He also observed that humblebees after trying to suck at the mouths of the flowers of Primula elatior, made holes through the corolla.

Dr. Ogle tells of an interesting experiment carried out in Switzerland. He gathered about a hundred flower-stems of the common blue variety of monkshood(Aconitum napellus), and not a single flower was perforated; he then gathered the same number of the white variety, and everyone of the open flowers had been perforated. "This surprising difference in the state of the flowers may be attributed with much probability to the blue variety being distasteful to bees, from the presence of the acrid matter which is so general in the Ranunculaceae, and to is absence in the white variety in correlation with the absence of the blue tint. "* According to Sprengel,"this plant is strongly protandous, it

* Dr. Ogle -- "Popular Sci. Review -- July 1869 -- Page 267

would therefore be more or less sterile unless bees carried the pollen from the younger to the older flowers. "*

Bees show much skill in their manner of working, for they always make their holes close to the spot where the nectar lies hidden within the corolla. The most remarkable case of skill and judgment was found in the perforation of the flowers of Lathyrus sylvestris described by Darwin. "The nectar in this plant is enclosed within a tube, formed by the united stamens, which surround the pistil so closely that a bee is forced to insert its proboscis outside the tube; but two natural rounded passages or orifices are left in the tube near the base, in order that the nectar may be reached by the bees."* The remarkable part of the observation was that the humblebees bite holes through the standard-petal, and they always worked on the left side over the passage, which is generally the larger of the two.

The motive which impels bees to perforate corollas seems to be the saving of time, for they lose a great deal of time climbing in and out of the flowers. O bservations have shown that bees could visit nearly twice as many flowers if they secured the honey in this way.

A fact in perforation which has been proved without a doubt is that the humblebees as a gneral rule perforate flowers only when they grow in large numbers near together. Hence it follows that the red clover and the common bean which are cultivated in large masses are eminently liable to be perforated. This fact is explained by the rich booty which is afforded by flowers growing in large numbers. Their conspicuousness attracts great crowds of these insects.

* "Das Entdeckte" Sprengel Page 278
* "Cross and Self Fertilization in the Vegetable Kingdom" Darwin Page 429

All plants suffer in some degree when bees obtain their nectar through the perforation of the corolla. The number of individuals reared is reduced and consequently the nectar supply is diminished. This results in the plant becoming rare and as it is not abundant enough to live in masses, the bees do not seek the nectar in an illegitimate manner.

SUMMARY

Pollination is the transfer of pollen from the anthers to the stigmas, the chief activity of the flower. The pollen may be transferred from the anthers to the stigma of the same flower, called close pollination or autogamy, or the pollen may be transferred from a flower of one plant to a flower of another, called cross pollination or xenogamy. Occurring between these two methods is geitonogamy, in which the pollen is transferred from one flower to another on the same plant.

Flowers are usually described as whorls of modified leaves which are involved in producing seeds. The essential parts consisting of the stamens and the pistil. The stamens produce the pollen which is greatly varied and well protected by the plant, either by the structure of the plant itself or by varied movements. The pistil consists of three distinct parts, the ovary, the style, and the stigma. The pollen comes to rest on the stigma, from which a tube grows down through the style of the pistil to the ovary, resulting in the formation of a seed.

Autogamy may occur through the direct contact of the anther and stigma, brought about by various movements and structures of the flowers. However, it has been proven that it is not as advantageous to the flower as a crossing of pollen and therefore many methods of prevention have been developed, including dichogamy, heterostyly, self-sterility, and various mechanical features of the flower itself.

Geitonogamy may be direct or indirect. The former method may be found in plants where the position of the stamens and pistil permits the pollen to fall directly upon the stigma. In the latter method the transfer is effected by the movement of the various organs of the flowers.

Xenogamy is only made possible by the action of external agents, which include principally, insects, wind, water, and birds. The simplest agency is the wind, the flowers pollinated by it being relatively simple and producing enormous quantities of pollen, thus providing for the immense waste of this method. Pollination aided by water is very commonly found in Potomogetonaceae and Najadadaceae. The most remarkable example of this type of pollination is found in the Italian eel-grass, Vallisneria spiralis. There is an interesting interrelation between birds and flowers, the most common pollinators include the pencil-tongued parrots, the tailor birds, the honey birds, the honey eaters, and the most important bird agent,-the humming birds. The birds are attracted by the brilliant colors, seeking the abundant nectar and in doing so transfer the pollen which they receive to other flowers on later visits.

The greatest of all agents in effecting cross pollination are the insects, many of which have developed in correlation with the forms of particular flowers. The flowers offer many inducements to the insects, for example, a place for the young, protection from storms, and most common, food, which includes nectar, pollen, and dusty, flour-like coverings which are similar to pollen in appearance. The insects may be attracted by the odor or the color of the flower, one excluding the other, as when

the color is the allurement, the scent is absent, and vice versa. In general, color has been proven to be the real guide to the flower, scent only being used to aid the insect in picking out the species it has been in the habit of visiting.

Bees are the most important pollinators, mainly due to their extensive activity, their precision, and their adaptations to the flowers. Flowers with long, slender tubes having the nectar secreted at the base of this tube, are well adapted to visits of moths and butterflies. The activity of the moths is well illustrated in the Yucca which is pollinated exclusively by the moth Pronuba yuccasella. Flies are usually attracted by the odors of flowers. The wasps of the family Chalcididae form an important agent in the transfer of pollen, especially in the Smyrna fig which depends on a small wasp, Blastophaga grossorum, for pollination.

Many mechanical mechanisms are found in plants to load the pollen on the visiting insects. These mechanisms include, percussive mechanisms, in which the filament strikes the insect like a hammer striking on a bell; explosive flowers, in which some organ of the flower springs up suddenly, scattering the pollen; and lastly, the sprinkling apparatus, in which the pollen is shaken out of the loculi where it is produced.

Many flowers possess numerous mechanisms by which the pollen is protected, both from wingless and winged marauders. Protection from wingless marauders may be classed into the following methods: isolation by water, sticky secretions, protection by glands and finally, protection by wax coatings. Winged marauders are kept

from the pollen by various means, including protection by floral structures, by hairs, by movements of the flower, and also by periodic display.

Many rarer agents have been found which have been proven to be real aids in the transfer of the pollen from one flower to another. These include bats, kangaroos, mosquitoes, and perhaps the rarest pollinators, the slugs and snails.

The perforation of the corolla of some plants has been found to be caused by humble bees. This illegitimate method of securing the nectar results in a non-production of seeds in many plants. Experiments have proven that bees save considerable time when they secure the nectar in this way. This fact has been offered as the motive which impels the bees to perforate the corolla when in search of the nectar.

The transfer of the pollen from the anthers to the stigmas, thus initiating the "promise of the plant that is to be," is one of the most fascinating studies of the plant world.

CROWFOOT FAMILY (RANUNCULACEAE)*

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
Virgin's Bower, or Virginia Clematis	Clematis Virginiana	Flies and short-tongued bees	Stigmatic flowers generally separate from staminate flowers
Liver-leaf, or Hepatica	Hepatica triloba	Pollen-collecting bees and flies	Some flowers perfect others stigmatic, and others staminate. Perfect flowers frequently self-fertilized
Sharp-lobed Hepatica	Hepatica acutiloba	Bees and flies	Stigmatic flowers sometimes separate from staminate ones.
Windflower, or Wood Anemone	Anemone nemorosa	Bees, beetles, and flies	Self-fertilization probably quite frequent.
Tall Meadow Rue	Thalictrum cornuti	Many insects	Some flowers perfect others staminate,
Common Meadow Buttercup	Ranunculus Acris	60 species noted	
White Baneberry	Actaea alba	Female bees Halistus	Tendency toward maturing stigma before anthers.
Black Cohosh	Cimicifuga racemosa	Pollen-gathering flies	
Marsh Marigold	Caltha palustris	Bees and flies beetles and butterflies	Anthers open outward.
Gold-thread	Coptis trifolia	Gnats and beetles	
Wild Columbine	Aquilegia vulgaris	Bumblebees, long-lipped bees, long-tongued bees.	Anthers mature before stigma. Flower has lost the power of self-fertilization.

*Gibson, W. H. Blossom Hosts and Insect Guests Pages 180-197

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
European, or Common Garden Columbine	Aquilegia Canadensis	Bumblebees and humming birds	Some anthers mature before stigmas.
Field, or Branched Larkspur	Delphinium Consolida	Bumblebees and butterflies	Anthers mature and wither before stigmas are mature. Flower has lost power of self-fertilization.
Tall Wild Larkspur	Delphinium exaltatum	Bumblebees	Anthers mature before stigma

MAGNOLIA FAMILY (MAGNOLIACEAE)

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
Laurel, or Small Magnolia	Magnolia glauca	Beetles	Stigma matures before anthers

BARBERRY FAMILY (BERBERIDACEAE)

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
Common Barberry	Berberis vulgaris	Bees	Pollen concealed in boxes, stamens liberated by the insects. Self-fertilization not probable

WATER-LILY FAMILY (NYMPHAEĈEAE)

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
Yellow Nelumbo	Nelumbo luteum	Small bees, flies, and beetles	Stigma matures before anthers.
Pond Lily	Nymphaea odorata	Pollen gathering bees and flies	Self-fertilization possible.
Water Lily	Nuphar advena	Small bees, flies, and beetles.	Stigma matures before anthers.

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
	POPPY FAMILY (PAPAVERACEAE)		
Blood root	Sanguinaria Canadensis	Short tongued bees and flies	Stigma matures before anthers.
	FUMITORY FAMILY (FUMARIACEAE)		
White Hearts	Dicentra cucullaria	Long-tongued female bumblebees	Anthers mature before stigmas.
Pale Corydalis	Corydalis glauca	Pollen-collecting bees, also humblebees seeking nectar	
	MUSTARD FAMILY (CRUCIFERAE)		
Field or Corn Mustard	Brassica Sinapis arvensis	Bees and flies	Anthers rotate away from stigma. Self-fertilization possible.
Ladies' Smock	Cardamine rhomboidea	Many insects	Anthers rotate way from stigma.
Spring Cress	Cardarome pratensis	Bees, flies	Stamens revolve away from stigma.
Crinkle-root	Dentaria diphylla	Pollen-collecting bees	
Whitlow grass	Draba verna	Pollen-collecting bees	Self-fertilization very common.
Shepherd's Purse	Capsella bursa-pastoris	Flies	Self-fertilization very common.

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.

VIOLET FAMILY (VIOLACEAE)

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
Arrow-leaved Violet	Viola sagittata	Bees	Showy flowers cross fertilized. Depends largely for the propagation of its kind upon cleistogamous buds
Blue Violet	Viola Cucullata	Small pollen collecting bees	Stigma remote from anther, but self-pollination possible.
Bird-foot Violet	Viola pedata	Long-tongued bees and butterflies	Protuding stigma strikes incoming bee. Pollen liberated, by the jar of insect's contact with the stigma, from the anther.
Sweet White Violet	Viola blanda	Bees	
Primrose-leaved Violet	Viola Primulaefolia	Bees	
Lance-leaved Violet	Viola lanceolata	Bees	
Canada Violet	Viola Canadensis	Bees	

ROCK-ROSE FAMILY (CISTACEAE)

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
Long-branched frostweed, or Frost flower	Helianthemum Canadense	Many insects	Stamens lie flat to petals well away from stigma

Common Name	Scientific Name	Insect Visitors	Method of Preventing or limiting self-fertilization, etc.
	ST. JOHN'S - WORT FAMILY (HYPERICACEAE)		
Common St. John's Wort	Hypericum perforatum	Pollen gathering bees. Pollen eating flies	Self-fertilization very common
Marsh St. John's Wort	Elodes Virginica	Same	Same
	PINK FAMILY (CARYOPHYLLACEAE)		
Deptford Pink	Dianthus armeria	Butterflies	Self-pollination probable
Corn-cockle	Lychnis githago	Moths, bees, butterflies, and flies	Anthers mature before stigma
Wild or Pink Catchfly	Silene Pennsylvanica	Bees, butterflies	Anthers mature before stigma, 2 sets of stamens maturing at different intervals
Fire Pink	Silene Virginica	Butterflies	
Starry Campion	Silene stellate	Moths and butterflies	
Bladder Campion	Silene inflata	Moths	Some flowers perfect, others staminate, and others stigmatic; Still others mature anthers and stigmas at different periods.
Soapwort, or Bouncing Bet	Saponaria officinalis	Sphinx Moth Pollen gathering bees	Anthers mature before stigmas, 2 sets of stamens maturing at different intervals.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Common Chickweed	Stellaria media	Small bees and flies	Has not lost the power of self-fertilization, though its anthers generally mature before its stigma.

PURSLANE FAMILY (PORTULACACEAE)

Spring Rose Beauty	Claytonia Virginica	Female bumblebees	Anthers mature before stigma

MALLOW FAMILY (MALVACEAE)

Swamp Rose Mallow	Hibiscus moscheutos	Bumblebees	Anthers mature before stigma
Common or Round-leaved Mallow	Malva rotundifolia	Mainly bees	Self-fertilization very common
High Mallow	Malva sylvestris	Many insects	Pistils radiate away from stamens. Stamens mature first.

GERANIUM FAMILY (GERANIACEAE)

Yellow Wood Sorrel	Oxalis stricta	Bees	Self-pollination usual.
White or True Wood Sorrel	Oxalis Acetosella	Few insects	Showy flowers incapable of self-fertilization produces also cleistogamous buds.
Violet Wood Sorrel	Oxalis violacea	Small bees	Dimorphic blossoms

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Wild or spotted Geranium	Geranium maculatum	Small bees	Anthers mature before stigma
Herb Robert or Red Robin	Geranium Robertianum	Flies	Anthers mature before stigma. Two sets of stamens. Evil-smelling flower.
Spotted Touch-me-not or Jewel Weed	Impatiens fulva	Bees, humming birds	Stigma concealed beneath stamens. Anthers mature first. Produces also cleistogamous buds

CASHEW FAMILY (ANACARDIACEAE)

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Staghorn Sumac	Rhus typhina	Short-tongued bees and flies	Stigmatic flowers generally separate from staminate ones.

STAFF-TREE FAMILY (CELASTRACEAE)

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Climbing Bitter-sweet	Celastrus scandens	Small bees and flies	Stigmatic flowers generally separate from staminate ones.

POLYGALA FAMILY (POLUGALACEAE)

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Common Field or Purple Milkwort	Polygala sanguinea	Bees	Produces both showy and cleistogamous buds
Racemed Milkwort	Polygala polygama	Bees	Fruiting organs within a tube split on the back to insure contact with bee.
Fringed Polygala	Polygala paucifolia	Bumblebees	Stamens and pistils are enclosed in keel, the two surfaces, however, turned in opposite directions. Produces also Cleistogamous buds.

PULSE FAMILY (LEGUMINOSAE)

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Wild Lupine	Lupinus perennis	long-lipped pollen-collecting bees	
Rattle box	Crotalaria sagittalis	bees	
White Sweet Clover	Melileotus-alba	Short-tongued bees	
Red Clover	Trifolium pratense	Bumblebees and butterflies	
Trailing bush Clover	Lespedeza procumbens	Bees	Produces also cleistogamous flowers.
Canadian or Showy Tick-trefoil	Desmodium Canadense	Bees	
Ground-nut, Wild Bean	Apios tuberosa	Butterflies and long-tongued bees.	Pulp between anthers and stigma.
Hog-peanut	Amphicarpaea monoica	Bees	Produces also cleistogamous buds.
Butterfly Pea	Clitoria mariana	Bees	
Beach Pea	Lathyrus maritimus	Long-tongued bees.	Self-pollination probable.
Cow Vetch	Vicia cracca	Flies, bees and butterflies	self-fertilization usual.
Wild False Indigo	Baptisia tinctoria	Bees	
Wild Senna	Cassis marilandica	Bumblebees	
Small Flowering Senna	Cassia nictitans	Pollen-gathering bumblebees	Anthers radiate from stigma.

ROSE FAMILY (ROSACEAE)

Common Name	Scientific Name	Insect Visitors	Methods of Preventing- or limiting self-fertilization, etc.
Meadow-sweet	Spiraea salicifolis	Bumble-bees	Stigma matures before anthers.
Nine-bark	Spiraea-opulifolis	Bees and flies	
Hard hack	Spiraea tomentosa	Pollen collecting bees	Self-fertilization common
Goats-beard	Spiraea aruncus	Bees, flies, and beetles	Some flowers perfect other staminate, and others stigmatic
Queen-of-the Prairie	Spiraea lobata	Butterflies and Bees	
Indian Physic	Gillenis trifoliata	Small long-tongued bees	
Pruple or Water Avens	Geum rivals	Bumblebees	Stigmas generally mature before anthers
White Avens	Geum album	Bees and flies	Stigma generally mature before anthers
Virginia Strawberry	Fragaria Virginiana	Several insects	Stigmatic flowers frequently separate from staminate.
Creeping Dalibarda	Dalibarda repens	Several	Produces both showy and cleistogamous buds
Virginia Raspberry	Rubus odoratus	Bumblebees	Outer anthers mature a little before stigmas, but self-fertilization from the inner row of anthers is common
Wild Red Raspberry	Rubus strigosus	Pollen-collecting bees	Self-fertilization is common

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
High Black-berry	Rubus villosus	Bumblebees	Stigma generally matures a little before anthers. Stamens turn away from stigma. Self-fertilization is common.
Common Agrimony	Agrimonia eupatoria	Flies and bees	Self-fertilization
Common Hawthorn	Crataegus coccinea	Flies and beetles	Self-fertilization
June Berry	Amelanchier Canadensis	Female bees	Self-fertilization

SAXIFRAGE FAMILY (SAXIFRAGACEAE)

Grass of Parnassus	Parnassis Caroliniana	Flies and bees	Anthers mature before stigma.
Early Sax-ifrage	Saxifraga Virginiensis	Flies and bees	Anthers mature before stigma.
False Mitrewort	Tiarella cordifolia	Bees	

ORPINE FAMILY (CRASSULACEAE)

Orpine, or Live-forever	Sedum telephium	Bees and flies	Anthers mature before stigma.

WITCH-HAZEL FAMILY (HAMAMELACEAE)

Witch-Hazel	Hamamelis Virginica	Bees and flies	Stigmatic flowers generally separate from staminate flowers.

EVENING-PRIMROSE FAMILY (ONAGRACEAE)

Enchanter's Nightshade	Circaea lutetiana	Bees and flies	Self-fertilization infrequent.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Fireweed	Epilobium angustifolium	Bumble-bees	Anthers mature before the stigma.
Evening Primrose	Enothera biennis	Moths	Anthers mature before the stigma.
Common Sundrop	Enothero fructicosa	Bumblebees and butter-flies	Stigmas protrude far beyond anthers.

MELASTOMA FAMILY (MELASTOMACEAE)

Meadow-Beauty	Rhexia Virginica	Bees	

LOOSESTRIFE FAMILY (LYTHRACEAE)

Spiked Loose-strife	Lythrum Salicaria	Butter-flies and bees	Trimorphic

CACTUS FAMILY (CACTACEAE)

Common Prickly Pear	Opuntia Vulgaris	Flies, bees and beet-les	Self-fertilization usual

GOURD FAMILY (CUCURBITACEAE)

Star-Cucumber	Sicyos angulatus	Several	Stigmatic flowers separate from stam-inate flowers.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.

PARSLEY FAMILY (CUCURBITACEAE)

Black Snake-root	Sanicula Marylandica	Several	Stigmas mature before anthers, which are imprisoned beneath the petals until all danger of self-fertilization is past. Some flowers perfect, others only staminate.
Common Carrot	Daucus Carota	Bees, flies, wasps, etc.	Stigmatic flowers on outer edge. Staminate flower grouped in center.
Sweet Cicely	Osmorrhiza longistylis	Flies and bees	Some flowers are perfect other staminate. In the perfect ones the anthers mature before the stigmas.
Water Hemlock	Cicuta maculata	Flies, bees, and wasps	Same as above
Cow-parsnip	Heracleum lanatum	Flies, bees, and wasps	Anthers mature before stigmas.

GINSENG FAMILY (ARALIACEAE)

Spikenard	Aralia racemosa	Flies and bees	Some flowers perfect others staminate, others stigmatic.
Common Wild Sarsaparilla	Aralia nudicaulis	Flies and bees	
Ginseng	Aralia quinque-folia	Several	Bears both showy and cleistogamous flowers.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
	DOGWOOD FAMILY (CORNACEAE)		
Flowering Dogwood	Cornus florida	Bees, flies, and butter-flies	Self-fertilization possible.
	HONEYSUCKLE FAMILY (CAPRIFOLICEAE)		
Twin-flower	Linnaea borealis	Bees, flies	Stigma protrudes, in advance of anthers
Coral or Trumpet Honey-suckle	Lonicera sempervirens	Humming birds	
Sweet Wild Honeysuckle	Lonicera grata	Sphinx moth	Stigma protrudes and receives incoming pollen
Bush-Honey-suckle	Diervilla trifida	Bees	Same as above
High Bush-Cranberry	Viburnum-Opulus	Small bees and flies	Insects cross-fert-ilize flowers mere-ly by crawling over the clusters
Hobblebush	Viburnum lantanoides	Small bees and flies	Insects cross-fert-ilize as above
Common Elder	Sambucus Canadensis	Pollen gath-ers, flies, beetles, and lesser bees.	Stamens radiate
	MADDER FAMILY (RUBIACEAE)		
Partridge-berry	Mitchella repens	Bees	Dimorphic blossoms
Button-bush	Cephalanthus occidentalis	Bees and butterflies chiefly	Anthers mature before stigma. The pollen is shed on the style be-fore the buds open. but is carried way by insects before the stigma matures

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Bluets	Houstonia caerulea	Flies, bees, and butterflies	Dimorphic flowers

TEAZEL FAMILY (DIPSACEAE)

Wild Teazel	Dipsacus sylvestris	Bumblebees	Anthers mature before stigma

COMPOSITE FAMILY (COMPOSITAE)

Common Burdock	Lappa officinalis	Butterflies and bumblebees	
Common Tansy	Janacetum vulgare	Bees, flies, beetles, and butterflies	
Pearly Everlasting	Antennaria margaritacea	Flies and beetles	Stigmatic flowers generally separate from staminate flowers
Iron-weed	Verononia noveboracensis	Butterflies and long-lipped bees	
Common Blazing-star	Liatris squarrosa	Long-tongued bees and flies	
Joe-Pye weed	Eupatorium purpureum	Butterflies and bees, flies	Anthers mature before stigma
Boneset	Eupatorium perfoliatum	Beetles, flies, wasps, and bees	
Groundsel-bush or tree	Senecio vulgaris	Very few insects bees chiefly	Stigmatic flowers frequently separate from staminate ones: self-fertilization usual, since many seeds are produced even in seasons unfavorable to insect visits.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Golden Ragwort	Senecio aureus	Many insects	
Elacampane, or Horseheal	Inula Helenium	Many insects	Disk florets contain both pistils and stamens, ray florets apt to be staminate only
Golden-rods	Solidiago	Many insects	Disk florets contain both pistils and stamens, ray florets apt to be staminate
Asters	Aster	Many insects	Self-fertilization frequent
Robin's Plantain	Erigeron bellidifolium	Bees and thistle butterfly	
Daisy-Flea-bane	Erigeron annuum	Many insects	Self-fertilization
Yarrow	Achillea millefolium	Bees, flies butterflies, and beetles	
Common May weed	Maruta cotula	Flies	Ray flowers neutral
Daisy	Chrysanthemum Leucanthemum	Numerous insects	Self-fertilization frequent in absence of insects
Sneezeweed	Helenium autumnale	Flies, and bees	Disk flowers contain both pistils and stamens, many florets apt to be stigmatic
Golden Coreopsis	Coreopsis lanceolata	Flies and butterflies	Disk flowers perfect ray-flowers without anthers or stigmas
Larger Bur-Marigold	Bidens chrysanthemoides	Many insects	Disk flowers perfect self-fertilization usual

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Tall Sunflower	Helianthus giganteus	Many insects	Disk flowers perfect self-fertilization usual
False Sunflower	Heliopsis laevis	Many insects	Disk flowers perfect self-fertilization usual
Black-eyed Susan	Rudbeckia hirta	Many insects	Disk flowers perfect self-fertilization usual
Tawny Hawkweed	Hieracium paniculatum	Flies and smaller bees	
Common Dandelion	Taraxacum dens-leonis	Many insects	Flowers of early spring and of late fall not visited by insects, but are fertile, self-fertilization common.
Sow Thistle	Sonchus arvensis	Many insects	Self-fertilization

LOBELIA FAMILY (LOBELIACEAE)

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Great Blue Lobelia	Lobelia syphilitica	Bumblebees	Anthers mature before stigmas, Stigmas protrude far beyond anthers

CAMPANULA FAMILY (CAMPANULACEAE)

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Venus's Looking Glass	Specularia perfoliata	Many insects	Produces both showy and cleistogamous flowers. Anthers mature before stigmas.
Common Harebell	Campanula rotundifolia	Bees and butterflies	Anthers mature before stigmas

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
	HEATH FAMILY (ERICACEAE)		
Trailing Arbutus	Epigaea repens	Bumblebees, flies, bees	In a transition state, showing a tendency toward trimorphism
Common Huckleberry	Gaylussacia resinosa	Small bees	Stigma protrudes
Andromeda	Andromeda floribunda	Small bees	Stigma protrudes
Mountain Laurel	Kalmia latifolia	Small bees	Anthers concealed in pocket
American Rhododendron	Rhododendron maximum	Small bees	
Purple Azalea	Azalea nudiflora	Small bees	Stigma protrudes
Wintergreen	Pyrola rotundifolia	Bees, Flies	Stigma protrudes
Spotted Pipsissewa	Chimaphila maculata	Bees, flies	Stigma protrudes
	HOLLY FAMILY (AQUIFOLIACEAE)		
Mountain Holly	Numopanthies Canadensis	Several	Staminate flowers separate from stigmatic ones.
Black Alder	Ilex verticillata	Several	Staminate flowers separate from stigmatic ones.
	PRIMROSE FAMILY (PRIMULACEAE)		
American Cowslip	Dodecathon Meadia	Bumblebees	Stigma protrudes

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Star-flower, or American Chick-weed	Trientalis Americana	Bees, flies	Stigma mature before the anthers
Lance-leaved Loosestrife	Lysimachia lanceolata	Bees	Stamens drawn away from styly by expanding petals during time stigma is receptive
Common Pimpernel	Anagallis arvensis	Pollen-collecting insects	Self-fertilization frequent

BLADDERWORT FAMILY (LENTIBULACEAE)

Large Bladderwort	Utricularia vulgaris	Bees, flies	As soon as the incoming insect fertilizes the stigma, it rolls up to prevent contact with its own pollen

BIGNONIA FAMILY (BIGNONIACEAE)

Wild Trumpet-flower	Tecoma radicans	Humming birds	Lobes of stigma close when touched

BROOM-RAPE FAMILY (OROBANCHACEAE)

Beech-drops	Epiphegus Virginiana	Several insects	Produces cleistogamous buds. Perfect flowers are sterile.

FIGWORT FAMILY (SCHROPHULARIACEAE)

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Common Mullein	Verbascum thapsus	Pollen-collecting bees and flies	Stigma protrudes and strikes the incoming bee.
Culver's Root	Veronica Virginica	Many insects	Anthers mature before the stigmas
Booklime	Veronica Americana	Many insects	Anthers mature before the stigmas
Common Speedwell	Veronica officinalis	Many insects	Growing in dense clusters, cross-fertilization is effected by insects, crawling over the head.
Broad-leaved Collinsia	Collinsia verna	Bees	Two sets of stamens maturing at different intervals.
Wild Toadflax	Linaria Canadensis	Long tongued bees and butterflies	
Butter-and Eggs	Linaria vulagaris	Bumblebees and butterflies	Stamens of two lengths.
Large Purple Gerardia	Geradia purpurea	Bees	Stigma protrudes
Downy False Foxglove	Geradia flava	Bumblebees	Stigma protrudes
Monkey Flower	Mimulus ringens	Long-tongued bees	Two sets of stamens and sensitive stigma which rolls up after contact with visitor, exposing stamens which then shed their pollen

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Figwort	Scrophularia	Wasps	Stigmas mature before anthers
Balmony	Chelone glabra	Bumblebees	Anthers mature before stigmas.
Hairy Beard Tongue	Pentstemon pubescens	Long tongued bees	Anthers mature before the stigmas.
Scarlet Painted Cup	Castilleia coccinea	Humming birds	
Wood Betony	Pedicularis Canadensis	Bees	

ACANTHUS FAMILY (ACANTHACEAE)

Hairy Rueillia	Ruellia ciliosa	Many insects	Bears both showy and cleistogamous buds

VERVAIN FAMILY (VERBENACEAE)

Blue Vervain	Verbena hastata	Bees and betterflies	

MINT FAMILY (LABIATAE)

Spear Mint	Mentha viridis	Many insects	Anthers mature before stigmas
Horsebalm	Collinsonia Canadensis	Bumblebees	Stigmas mature before anthers
Creeping Thyme	Thymus Serpyllum	Bumblebees, flies and butterflies	Some flowers perfect, other staminate, others stigmatic

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Oswego Tea	Monarda didyma	Bumblebees, flies and butterflies	
Wild Bergamont	Monarda fistulosa	Bumblebees, flies and butterflies	Anthers mature before stigmas.
Ground Ivy	Nepeta Glechoma	Many insects	Anthers and stigmas mature at different times.
False Dragon-Head	Physostegia Virginiana	Bumblebees	Anthers mature before stigma.
Self-Heal	Brunella vularis	Bumblebees	Anthers mature before stigma.
Skullcap	Scutlellaria lateriflora	Bees	Anthers mature before stigma.
Common Motherwort	Leomurus Cardiaca	Bumblebees	Two lengths of stamens.

BORAGE FAMILY (BORRAGINACEAE)

Viper's Bugloss	Echium vulgare	67 species	Anthers mature before stigma.
Cowslip	Mertensia Virginica	Many insects	Anthers widely separated form stigma.
True Forget-me-not	Myosostis palustris	Flies or bees	Anthers and stigma so arranged that they are touched by opposite sides of the tongue of the visiting insect.
Common Hounds-tongue	Cynoglossum officinale	Bees and butterflies	Self-fertilization possible.
Beggar's Lice	Cynoglossum morisoni	Pollen gathering bees	

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
	WATERLEAF FAMILY (HYDROPHYLLACEAE)		
Virginia Waterleaf	Hydrophyllum Virginicum	Bumblebees	Anthers mature before stigmas.
	POLEMONIUM FAMILY (POLEMONIACEAE)		
Sweet William	Phlox maculata	Butterflies	Anthers mature before stigmas.
Downy Phlox	Phlox pilosa	Butterflies	Anthers mature before stigmas.
Moss Pink	Phlox subulata	Butterflies	Anthers mature before stigmas.
	CONVOLVULUS FAMILY (CONVOLVULACEAE)		
Morning-glory	Ipomoea purpurea	Bees	Stigmas matures before anthers.
Wild Potato Vine	Ipomoea pandurata	Bumblebees	
Great Bind-weed	Calystegia sepium	Bees, moths, and beetles	Self-fertilization possible.
Field Bind-weed	Convolvus arvensis	Bees, flies, and beetles	Stigmas protrude beyond anthers. Self-fertilization possible owing to drooping position of flower.
	NIGHTSHADE FAMILY (SOLANACEAE)		
Black or Common Night-shade	Solanum nigrum	Pollen-gathering bumblebees	

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Ground Cherry	Physalis Pennsylvanica	Bees	Stigma matures before anthers, also protrudes beyond them.
Common Thorn-apple	Datura Stramonium	Sphinx moth	

GENTIAN FAMILY (GENTIANACEAE)

Rosy Centaury	Sabbatia angularis	Many insects	Anthers mature before stigma and open outward.
Fringed Gentian	Gentiana crinita	Bees and bumblebees	Anthers mature before stigma and open outward.
Closed Gentian	Gentiana Andrewsii	Bumblebees	Anthers mature before stigma and open outward.

DOGBANE FAMILY (APOCYNACEAE)

Spreading Dogbane	Apocynum androsaemifolium	Bees, flies	Pollen concealed in V-shaped cavity well away from stigma.
Indian Hemp	Apocynum cannabinum	Bees, flies, and beetles	Pollen concealed in V-shaped cavity well away from stigma.

MILKWEED FAMILY (ASCLEPIADACEAE)

Butterfly-weed	Asclepias tuberosa	Butterflies	Pollen concealed in V-shaped cavity well away from stigma.
Common Milkweed	Asclepias cornuti	Bees, flies and butterflies	Pollen concealed in V-shaped cavity well away from stigma.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
	BIRTHWORT FAMILY (ARISTOLOCHIACEAE)		
Wild Ginger	Asarum Canadense	Flies	Stigmas matures before anthers.
	POKEWEED FAMILY (PHYTOLACCACEAE)		
Pokeweed	Phytolacca decandra	Bees, flies	Anthers generally mature before stigma.
	BUCKWHEAT FAMILY (POLYGONACEAE)		
Common Persicaria	Polygonum Pennsylvanicum	Bees, flies	
	LIZARD'S TAIL FAMILY (SAURURACEAE)		
Lizard's tail	Saururus-cernuus	Flies	
	LAUREL FAMILY (LAURACEAE)		
Spicebush	Lindera-Benzoin	Many insects	Stigmatic flowers generally separate from staminate ones.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
	SPURGE FAMILY (EUPHORBIACEAE)		
Flowering Spurge	Euphorbia corollata	Flies	Staminate flowers separate from stigmatic ones.
	ARUM FAMILY (ARACEAE)		
Jack-in-the-Pulpit	Arisaema triphyllum	Gnats and other insects	
Water Arum	Calla-palustrus	Small insects	Lower flowers staminate and stigmatic. Upper flowers staminate only. Stigma matures before anthers.
Skunk Cabbage	Symplocarpus foetidus	Small flies	Stigma matures before anthers. Anthers turned away from pistil.
Golden Club	Orontium aquaticum	Flies	Cross-fertilized by insects crawling over it.
	WATER-PLANTAIN FAMILY (ALISMACEAE)		
Water Plantain	Alisma plantago	Flies	Stamens radiate away from stigma.
Broad-leaved arrow-head	Sagittaria variabilis	Bees and flies	Stigmatic flowers separate from staminate ones.
	PICKEREL-WEED FAMILY (PONTEDERIACEAE)		
Pickerel-Weed	Pontederia cordata	Bees and flies	Trimorphic

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
	ORCHID FAMILY (ORCHIDACEAE)		
Showy Orchid	Orchis-spectabilis	Bumblebees	
Fringed Orchid	Habenaria psycodes	Butterflies	
Ragged Orchid	Habenaria lacera	Butterflies	
Great Green Orchid	Habenaria orbiculata	Butterflies and smaller moths	
Rattlesnake Plantain	Goodyera	Bees	
Arethusa	Arethusa-bulbosa	Bees	
Pogonia	Pogonia ophioglossoides	Bees	
Moccasin Flower	Cypripedium acaule	Bees and bumblebees	
	AMARYLLIS FAMILY (AMARYLLIDACEAE)		
Yellow Star Grass	Hypocis erecta	Small bees and flies	Stamens radiate from stigma.
	SMILAX FAMILY (SMILACEAE)		
Carrion Flower	Smilax herbacea	Flesh flies	Staminate flowers separate.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
	IRIS FAMILY (IRADACEAE)		
Larger Blue Flag	*Iris versicolor*	Bees and bumblebees	Stigmatic surface covered by flexible flap, which insect opens as it withdraws proboscis and body from flower, Anthers face away from stigma.
	LILY FAMILY (LILLIACEAE)		
Great Flowered White Trillium	*Trillium grandiflorum*	Bees	Anthers mature before stigma.
Purple Trillium	*Trillium erectum*	Flesh flies and beetles	Evil smelling, Self-fertilization possible.
Nodding Trillium	*Trillium cernuum*	Bumblebees	Anthers mature before stigma.
Indian Cucumber-root	*Medeola Virginica*	Many insects	Styles much longer than stamens.
Blazing Star	*Chamaelirium luteum*	Many insects	Stigmatic flowers on separate plants from the staminate ones.
American White Hellebore	*Veratrum viride*	Flies	Anthers matures before stigmas.
Bellwort	*Uvularis perfoliata*	Female bees and bumblebees	Stigma protrudes.
False Solomon's Seal	*Smilacina racemosa*	Bees	Stigma matures before anthers.
Smaller Solomon's Seal	*Polygonatum biflorum*	Bees	Self-fertilization frequently.

Common Name	Scientific Name	Insect Visitors	Methods of Preventing or limiting self-fertilization, etc.
Wild Orange-Red Lily	Lilium Philadelphicum	Bees	
Canada Lily	Lilium superbum	Bees, and butterflies	Drooping position of flower renders self-fertilization difficult.
Turk's Cap	Lilium superbum	Bees, and butterflies	Drooping position of flower renders self-fertilization difficult.
Dog-toothed Violet	Erythronium Americanum	Small bees, butterflies, and flies	Self-fertilization common.
Wild Hyacinth	Scilla fraseri	Bees, flies, and butterflies	

SPIDERWORT FAMILY (COMMELYNACEAE)

Virginia or Common Day Flower	Commelyna Virginica	Pollen-collecting bees	
Spiderwort	Tradescantia Virginica	Pollen collecting bees	Stigma separated from anthers, extending so far beyond them that self-fertilization is improbable.*

*Gibson, W.H. -- Blossom Hosts and Insect Guest -- Pages 180-197

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